Forest Ecology and Management 417 (2018) 167–183

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tamm review

Tamm review: The North-American lichen woodland

Serge Payette[a,*], Ann Delwaide[b]

[a] Département de biologie and Centre d'études Nordiques, Université Laval, 1045, av. de la Médecine, Quebec City, Quebec G1V 0A6, Canada
[b] Département de géographie, Université Laval, 2405, rue de la Terrasse, Quebec City, Quebec G1V 0A6, Canada

ARTICLE INFO

Keywords:
Boreal forest
Cladonia
Caribou
Chronosequence
Fire
Frost
Lichen
Microclimate
Subarctic
Succession
Woodland

ABSTRACT

The lichen woodland (LW) is an open-crown subarctic forest distributed principally in North America where it extends from Newfoundland in Atlantic Canada to the Yukon and Alaska. It is the main tree ecosystem of the LW zone north of the closed-crown boreal forest zone, and south of the forest-tundra zone where its cover diminishes progressively toward the Arctic tree line. Growth and development of LWs are closely dependent on dry-mesic, nutrient-poor podzolic soil environments largely distributed on the Canadian Precambrian Shield. The sun-exposed open structure and dominance of lichen species on the dry-mesic soils of LWs determine many of their functions. A diversified cryptogamic flora is thriving in LWs due to reduced competition from vascular plants unable to grow and survive on dry, nutrient-poor soils. Because of the reduced greenhouse effect caused by the open structure and dominance of pale-color lichen mats inducing a greater albedo, LWs exerts a negative microclimatic impact on the environment culminating in the reduction of the frost-free growth season and increase and intensity of frost events. A suite of common, often recurrent, sometime compounding, fine- and large-scale disturbances (including climate change) activates the successional dynamics of LWs and also their historical and present expansion and contraction across the boreal biome. Post-disturbance chronosequences induced by fire, wind and caribou trampling and grazing are producing similar seral communities converging toward the self-maintenance of the LW ecosystem. Long-term succession in southernmost LW sites possibly converges toward the closing of tree canopy and recovery of closed-crown conifer forests (CCCF) in absence of fire. The creation of LW occurred repeatedly during the late Holocene, as well as its extirpation from the northernmost sites (forest-tundra zone) with wildfire as the principal triggering mechanism. LWs are presently unable to transgress the tree line, except for minor advances in small confined sites. Current evidence of the dual distribution of LWs and CCCF in eastern Canada shows that the LW zone is expanding southward into the CCCF zone, where compound disturbances associated with epidemics followed by small to extensive fires are transforming dense forest stands to LWs, a process most likely independent of climate. In terms of ecosystem management, there are concerns about the maintenance of the southernmost LWs within the CCCF zone as poor carbon sinks. Projects involving LW plantation sites in the CCCF zone in eastern Canada are proposed to offset the increased emission of atmospheric gases and thus mitigate climate change.

1. Introduction

Lichen-dominated ecosystems cover approximately 8–10% of the earth's terrestrial surface, particularly in subarctic and arctic regions (Crittenden, 1999). Among these ecosystems, the lichen woodland (LW), an open-crown subarctic forest, stands as the second largest ecosystem of the North American boreal biome, covering about 2 million km^2 in Canada (Johnson and Miyanishi, 1999). LWs extend from the Atlantic coast to the Rocky Mountains and the Yukon (Hustich, 1951, 1966; Hare, 1950, 1959; Rousseau, 1952, 1968; Hare and Ritchie, 1972; Rowe, 1972, 1984; Payette, 1983, 1992; Timoney, 1988; Timoney and Wein, 1991; Sirois 1992; Timoney et al., 1993; Payette et al., 2001), where they progressively decline in extent (Fig. 1). The rare LWs in Alaska are located on dry, acid, glacial deposits of the Brooks Range (Christiansen, 1988). The zonal distribution of LWs lies north of the closed-crown conifer forest, the largest conifer ecosystem of the continent (Brandt, 2009), which is dominated by black spruce (*Picea mariana* (Mill. B.S.P.), white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and balsam fir (*Abies balsamea* (L.) Mill.). The LW is the main forest ecosystem of the LW zone north of the closed-crown forest zone, and south of the forest-tundra zone where its cover diminishes progressively toward the Arctic tree line. In the forest-tundra zone, LWs are forming a complex spatial

* Corresponding author.
E-mail address: Serge.payette@bio.ulaval.ca (S. Payette).

https://doi.org/10.1016/j.foreco.2018.02.043
Received 8 February 2018; Received in revised form 23 February 2018; Accepted 26 February 2018
Available online 15 March 2018
0378-1127/ Crown Copyright © 2018 Published by Elsevier B.V. All rights reserved.

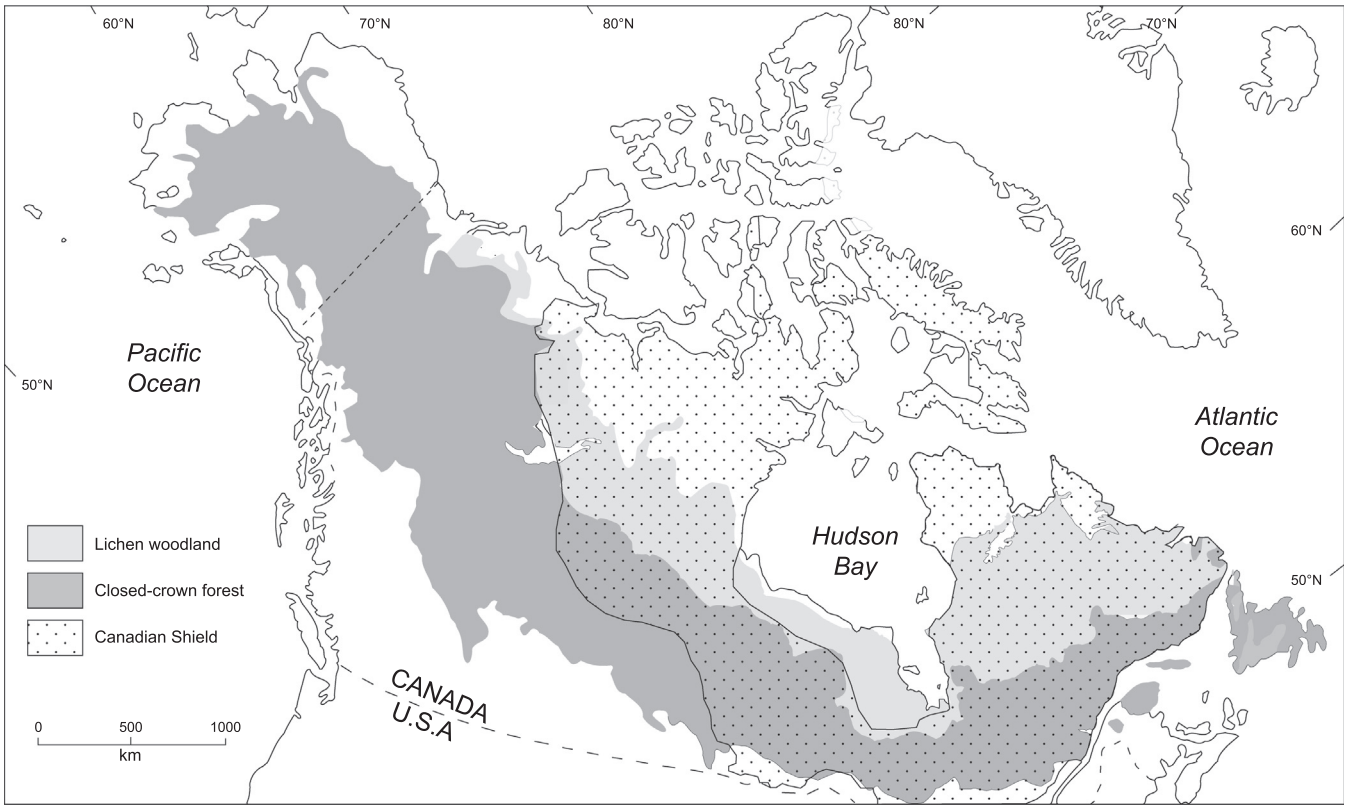

Fig. 1. Distribution of lichen woodlands in North America. Most lichen woodlands are growing on soils of the Precambrian Shield, except in Newfoundland, Yukon and a part of northern Ontario where Paleozoic rocks dominate.

pattern with lichen-tundra communities (Payette et al., 2001).

The LW zone extends northward to the Arctic treeline, and as such is a direct vegetational response to cold climatic conditions generated by moving air masses on both sides of the Arctic front (Bryson, 1966; Barry, 1967; Bryson and Hare, 1974; Johnson and Miyanishi, 1999). Yearly and seasonal precipitations do not appear to be the main causal factor of the distribution of lichen-dominated terrain across the continent. However, the boreal forest of northeastern North America receives more than twice the mean annual precipitation of its central and western counterparts (from 300 to 500 mm in central Canada to at least 600–1000 mm in Quebec-Labrador) (D'Orangeville et al., 2016). Even though the main geographical range of the LW is centered in the subarctic zone, its very existence is primarily dependent on the soil environment. This nutrient-poor ecosystem thrives on acid (pH < 4.5), relatively dry, coarse, sandy and rocky soils of the Canadian Precambrian Shield, and its continental distribution exceeds the boundaries of this major geological landmass only in the Yukon, northern Ontario and Newfoundland (Fig. 1). Outside North America, LWs are scattered across boreal Eurasia. Most LWs are dominated by Scots pine (*Pinus sylvestris* L.), mountain birch (*Betula pubescens* Ehrh.) and Siberian larch (*Larix sibirica* Ledeb.), on dry, coarse-grained soils of the Baltic Shield in northern Fennoscandia, and on acid and dry deposits of the Kola Peninsula and western Siberia (Steijlen et al., 1995; Tishkov, 2002; Tømmervik et al., 2004), respectively.

Conifer species growing in LWs are occasionally accompanied by broadleaf tree species such as paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.). The most extensive LWs are those occupied by black spruce and jack pine, whereas lodgepole pine, tamarack and white spruce LWs are less common (Figs. 2 and 3) (Morin and Payette, 1984; Rowe, 1984; Delwaide and Filion, 1988; Desponts and Payette, 1992; Coxson and Marsh, 2001; Houle and Filion, 2003; Laliberté and Payette, 2008). In eastern Canada, jack pine LWs generally grow outside the range of the subarctic LW zone (Rudolph and Laidly, 1990; Conkey et al., 1995; Barton and Grenier, 2008; Payette et al., 2017). Finally, pitch pine (*Pinus rigida* Mill.) LWs of the New Jersey pinelands are among the southernmost forest communities where lichens grow freely in close association with mosses (Sedia and Ehrenfeld, 2003).

In this review, we examine the main characteristics (structure, botanical composition, etc.), functions (microclimate, fire and animal interactions, spatiotemporal dynamics, etc.) and origin of LWs at several spatiotemporal scales. The regeneration potential and development of the LW ecosystem throughout the Holocene is assessed relative to its resilience to abiotic and biotic disturbances. Finally, we evaluate whether or not the geographical range of the LW ecosystem is changing relative to present climate warming. Conservation and management of LW are briefly discussed in the context of the C sink/source dynamics of boreal ecosystems.

2. Structure and plant composition of the lichen woodland

The floristic composition of LW includes a predominance of circumboreal and North-American boreal species. While no endemic species are exclusive to the LW ecosystem, a few arctic-alpine species currently grow in the northernmost exposed LWs at the Arctic treeline. The open structure of LW (generally 10–40% tree cover, including lichen parkland, with < 10% tree cover, Fig. 3) includes only a small number of mature trees compared to dense conifer forests, a contrasted difference of tree cover recorded in surface pollen assemblages across the boreal biome (King, 1993). Whereas the mean number of trees > 9 cm at breast height in > 100 year old dense spruce-moss forests is 1000–1050 stems ha^{-1} (based on a survey of 94 stands, Quebec Government Forest Surveys, 2013), the mean is only 560 stems ha^{-1} in LWs > 100 year old (based on a survey of 125 stands, Quebec Government Forest Surveys, 2013). These figures are similar to those of Rencz and Auclair (1978), who calculated a mean tree density of 556

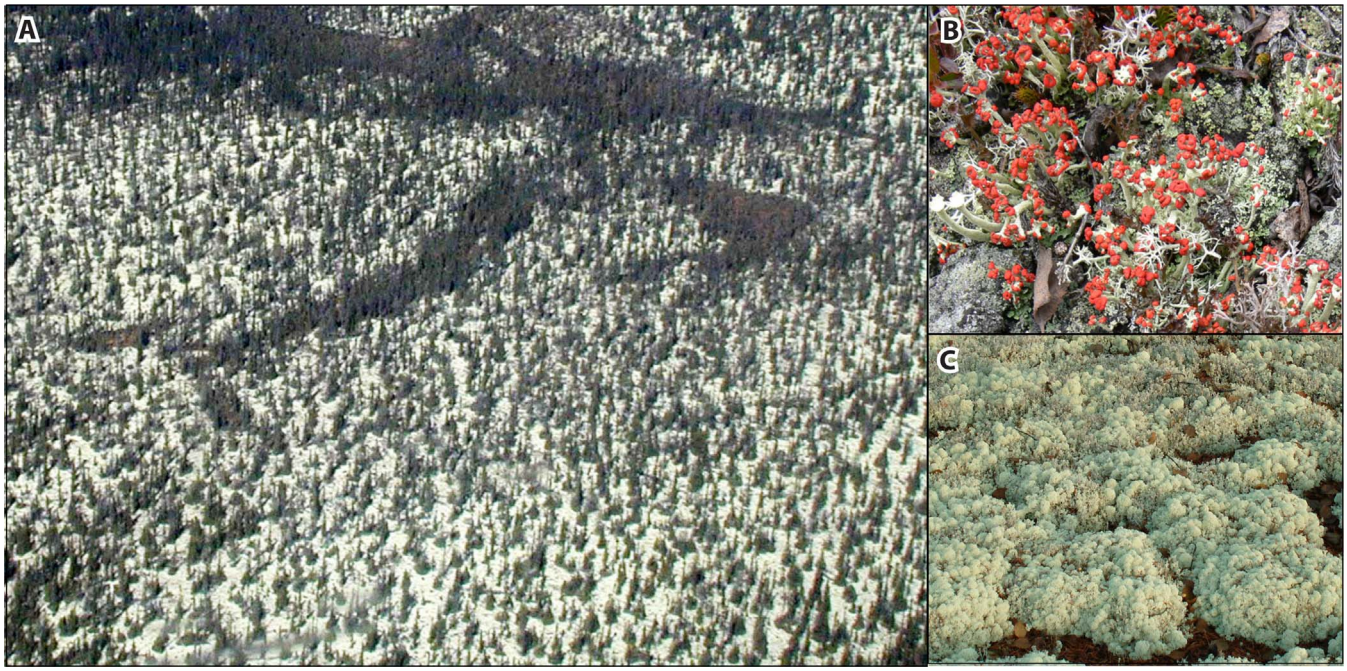

Fig. 2. (A) The lichen woodland ecosystem with sparse black spruce trees established after fire. (B) early successional lichen species, *Cladonia mitis*, *Cladonia deformis*, *Cladonia cristatella* and *Stereocaulon paschale*. (C) late successional lichen species, *Cladonia stellaris* forming polygonal lichen mats.

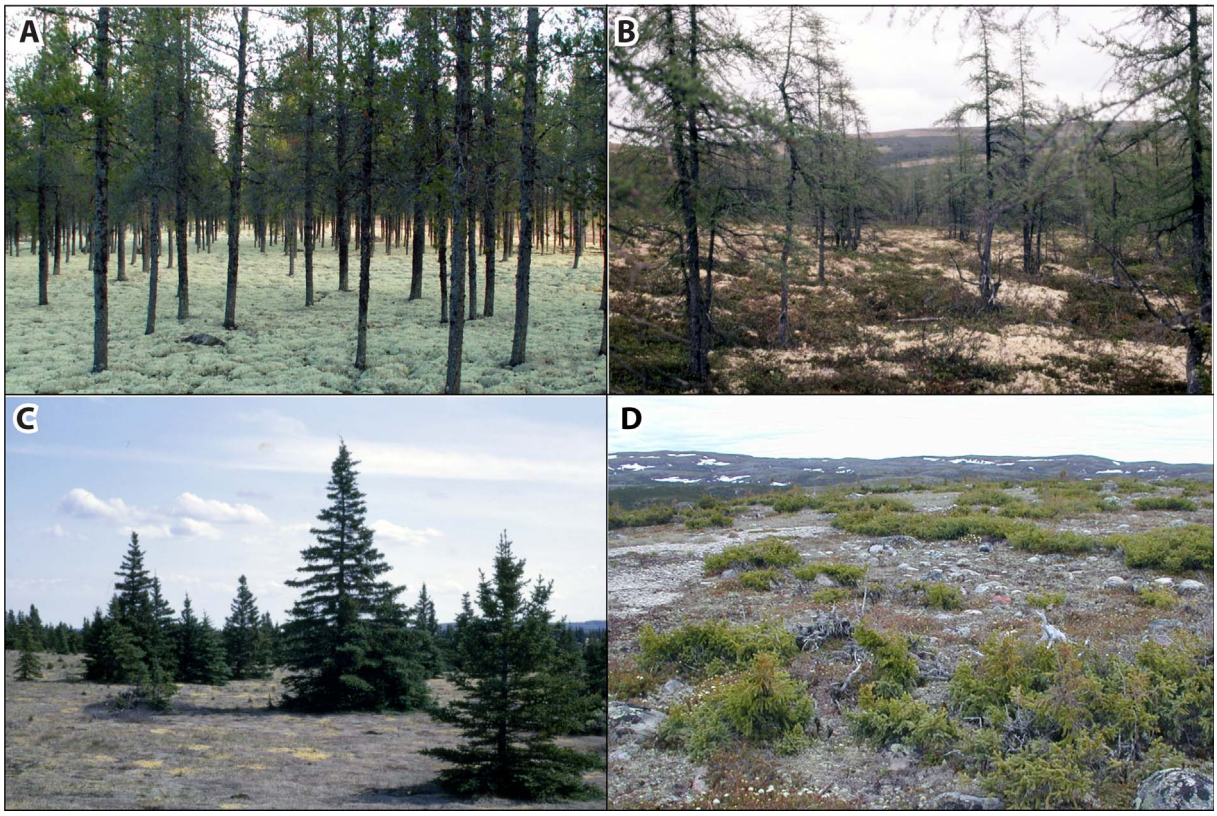

Fig. 3. Types of lichen woodland. (A) 77 year-old jack pine lichen woodland (1941 fire, James Bay area). Exclusive dominance of *Cladonia stellaris* and exclusion of vascular species because of deep burning of the organic horizon. (B) Eastern larch (*Larix laricina*) lichen woodland at the Arctic tree line, northern Quebec). (C) White spruce (*Picea glauca*) lichen woodland. Dominance of *Stereocaulon paschale* (in grey) because of sand saltation from nearby active dunes along the eastern coast of Hudson Bay. (D) Shrubby lichen woodland (or krummholz) dominated by black spruce (*Picea mariana*), *Cladonia stellaris* and *Rhododendron subarcticum* Harmaja. This very old-growth krummholz is maintaining at equilibrium in a fire-free environment at the Arctic tree line in north-western Quebec.

trees ha^{-1} in 15 LWs of the Schefferville area (subarctic Quebec). Mature trees in LW rarely exceed 10–15 m in height (Auclair, 1985; Girard et al., 2011; Côté et al., 2014).

The intertree distance in LW and lichen parkland generally varies between 5 and 20 m (Figs. 2 and 3). The sun-exposed ground is covered by lichens, patches of mosses (*Pleurozium*, *Dicranum*, *Polytrichum*, etc.), evergreen (*Rhododendron groenlandicum* (Oeder) Kron & Judd, *Kalmia angustifolia* L., *Vaccinium vitis-idaea* L., *Empetrum hermophroditum* Hagerup, *Arctostaphylos uva-ursi* (L.) Sprengel, etc.) and deciduous (*Vaccinium angustifolium* Aiton, *Vaccinium uliginosum* L., *Betula glandulosa* Michx., *Salix* spp., etc.) shrubs, and scattered pteridophytes (*Diphasiastrum complanatum* (Linnaeus) Holub, *Diphasiastrum sitchense* (Ruprecht) Holub, *Lycopodium annotinum* L., *Lycopodium dendroideum* Michx., *Lycopodium lagopus* (Laestadius *ex* C. Hartman) G. Zinserling *ex* Kuzeneva, etc.) (Figs. 2 and 3). The number of vascular species in LW at the local and landscape scales does not generally exceed 10 and 30 species, respectively. However, the cryptogamic flora is diversified, with several dozen species among which the genus *Cladonia* is the main taxon. Of the 128 *Cladonia* species occurring in North America (Brodo et al., 2001) which have circumboreal and circumpolar ranges (Thomson 1967), at least 30 species of terricolous *Cladonia*, including 4 fruticose species of the subgenus *Cladina*, currently grow in LWs (Fig. 2). *Cladonia mitis* Sandst., *Cladonia rangiferina* (L.) F.H.Wigg. and *Cladonia stellaris* (Opiz.) Pouzar & Vězda are the most frequent and abundant mat-forming species in LW. *Cladonia stellaris* is the iconic example of a mat-forming lichen present in LW and possibly one of the world's most frequent fungi (Crittenden, 1999). Light is the most significant growth-limiting factors of most *Cladonia* species (Ahti 1961). *Cetraria islandica* (L.) Ach., *Alectoria ochroleuca* (Hoffm.) A. Massal., *Bryocaulon divergens* (Ach.) Kärnefelt, *Stereocaulon paschale* (L.) Hoffm. and several other lichen species also grow on sun-exposed ground in LW, whereas mosses (*Pleurozium schreberi* (Willd. *ex* Brid.) Mitt., *Dicranum* spp., etc.) and liverworts (*Ptilidium ciliare* (L.) Hampe) are distributed in shady microenvironments provided by dwarf birch (*Betula glandulosa*), ericaceous shrubs, and conifer trees.

Similar to *Sphagnum* mosses, the growth habit of mat-forming lichens is unusual, as the secondary thallus grows vertically, whereas the podetial base dies, accumulates and decays rapidly (Sveinbjörnsson, 1987; Boudreau and Payette, 2004a). Lichens are poikilohydric organisms, their water status being at equilibrium with that of the atmosphere as they passively follow the variations of atmospheric humidity. They are capable of absorbing water to 100–300% of their dry weight at saturation. Lichens are effective in absorbing soluble and insoluble mineral materials from their surroundings. Their poikilohydrous water relations with wetting and drying cycles presumably accelerate the uptake of soluble minerals within the substrate by the mechanism of diffusion (Nieboer et al., 1978).

Low soil temperature is the main factor inhibiting decomposition of organic matter in LW soils (Moore, 1981). During the summer, soil temperature beneath the lichen mat rarely rises above 15 °C, though much higher temperatures can occur on the surface of recently burned sites (Lucarotti, 1976; Rouse, 1976; see section on LW microclimate below). Acid soils of spruce LWs have very low nitrogen (N) and macronutrient contents (including phosphorus, P, calcium, Ca, magnesium, Mg, and potassium, K) (Moore, 1980, 1984). A large proportion of the organically bound nutrients are stored in the organic horizon because of the slowly decomposing organic matter (Rencz, 1976; Moore, 1984). Comparative analysis of soil profiles highlight the low intrinsic fertility of LWs as well as their biological control of C, N, and mineral nutrients (Ouimet et al., 2018). Total C storage in the first 1 m of mineral soil profile is 2.4 times larger in closed-crown forest sites than in LW sites. Also, total soil (organic + mineral horizons) amounts of C, N and exchangeable Ca and Mg are 1.3–2.6 times greater in closed-crown forest sites than in LW soils.

Although the primary sources of N for lichen growth are telluric precipitation, dust particles and gases, lichenized blue-green algae are among the principal agents of N fixation on dry terrain of the Arctic and Subarctic through leaching of metabolites and decomposition of the thallus (Crittenden and Kershaw, 1978). *Stereocaulon*, *Peltigera* and *Nephroma* lichens contain cyanobacteria, and are the principal producers of N fixation in LW. Because of low rates of decomposition and mineralization of subarctic soils, fixed N from cyanophylic lichens is sequestered in organic horizons and released only by fire. Fires trigger rapid cycling of nutrients locked up in the biomass and organic ground layer (MacLean et al., 1983). However, fires have a minimal and short-lived effect on soil nutrient status (Moore, 1980, 1984) compared to the pronounced nutrient flush in other ecosystems. N-fixing lichens are said to improve the nutrient status of young and mature trees (Crittenden, 1983).

Maximum rates of respiration and photosynthesis by LW are one-quarter to one-half of those observed in temperate deciduous forests (Fan et al., 1995). Due to non-transpiring organisms, the lichen surface is relatively resistant to evaporation. Low daily totals of evaporation (< 3 mm per day) are recorded over jack pine and spruce LWs (Fitzjarrald and Moore, 1994) as a function of temperature, with 0.5–1.0 mm at 10 °C and 2.0–2.5 mm at 15–20 °C. *Cladonia stellaris* thallus shows stratified resistance to water loss, and its effective mulching properties produce greater water availability under the lichen mat (Kershaw and Rouse, 1971). Ericaceous plants (*Rhododendron*, *Vaccinium*, *Arctostaphylos*, *Kalmia*, etc.) in LW benefit from P uptake even from P-depleted soils through endomycorrhizal associations (Crawford, 1989).

3. The frost code of lichen woodlands

The diversified vegetation cover of the boreal landscape forms a network of microclimates with tremendous variability in energy exchange and balance (Karlsson, 2000; Geiger et al., 2003). Surface reflectivity or albedo is a central factor when comparing ecosystem microclimates at various spatial scales (Betts, 2000; Geiger et al., 2003; Bernier et al., 2011). The microclimatic signature of the main boreal forest vegetation types expressed in terms of energy transfer and balance depends on density of tree cover, functional type and topographic position. The open structure and botanical composition of the LW ecosystem determine many of its functions, in particular the microclimate. The architecture of the landscape as it is shaped by topography and the structure and composition of the dominant cover types constitutes the medium that receives, emits and transfers daily energy inputs and outputs. Hence, in the North-American boreal landscape, closed-crown conifer forests (CF) and LW with nearby lichen hollows (LH, or frost hollows) form a complex spatial assemblage that creates propitious conditions for heat exchange. LH are treeless, lichen-dominated communities occupying well-drained topographic lows always encircled by LWs (Dy and Payette, 2007).

Frost frequency and intensity As shown in a 19-year (1997–2015) study monitoring temperature in Grands-Jardins National Park (southern Quebec) (see Methods section), the climatic impacts generated by the biophysical structure of CF (90% tree cover), LW (25% tree cover) and LH (0–1% tree cover) are considerable in terms of temperature variability (Fig. 4). At the scale of the growing season, from June to August (92 days), the main structural features of each of these communities induce a distinct microclimate that results from the differential production and incursion of freezing air. Frost frequency (number of frost days during the June–August growing season, i.e., 92 days) is low in CF (1.9 ± 2.4%), whereas it is moderate in LW (9.6 ± 4.4%) and high in LH (32.7 ± 8.3%). Freezing in LH occurs about every two days in June (43 ± 12%), and also frequently during the warmest months of the year, i.e., 27 ± 6% and 30 ± 12% of the time in July and August, respectively. Because of the greenhouse effect created by the tree canopy, the frost-free period (number of days ≥ 0 °C) in CF (86 ± 6 days) is about two times longer than that of LW (49 ± 17 days). LH communities are found in harsh environments with

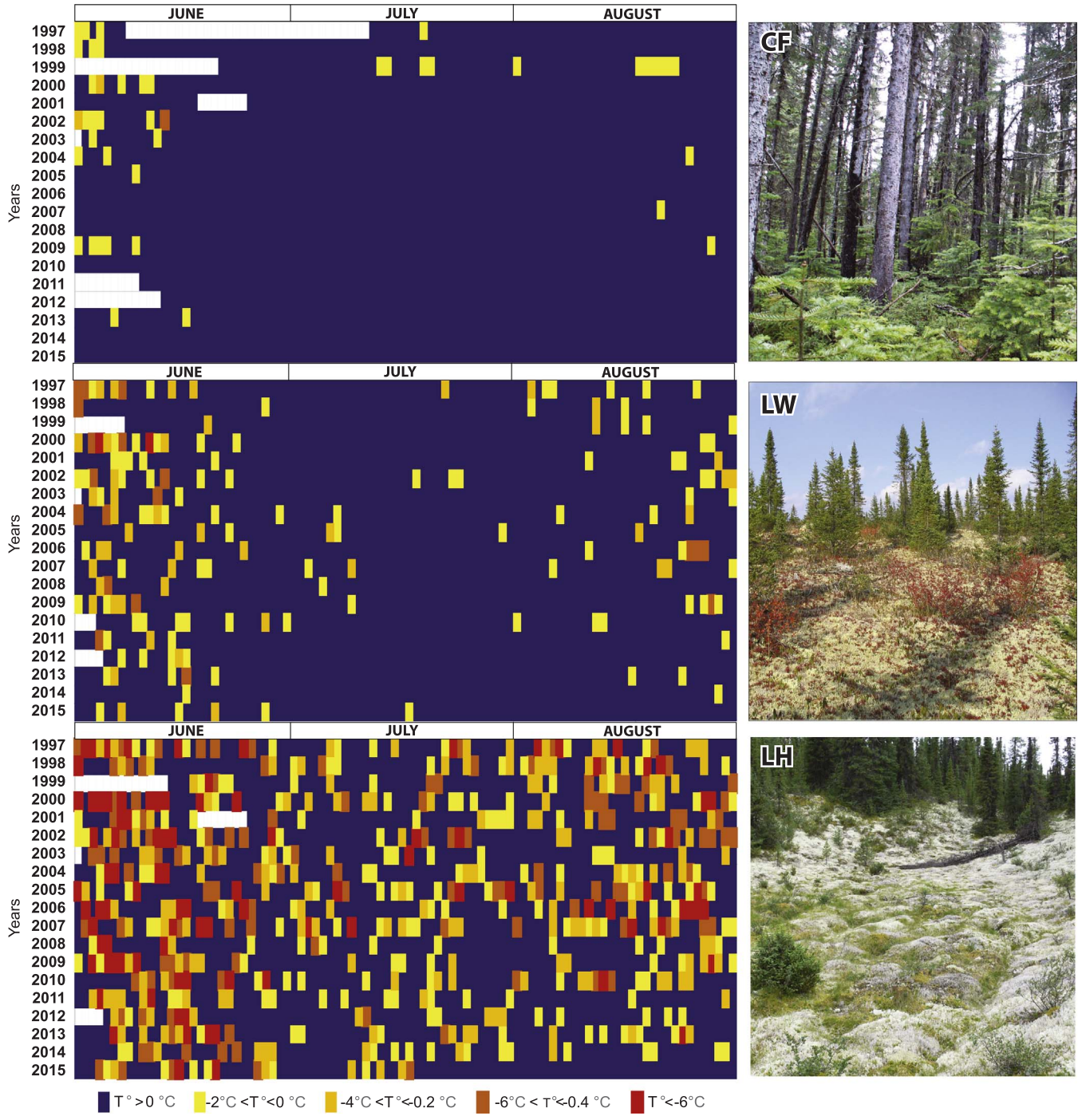

Fig. 4. Daily occurrences of frost events during the growing season from June to August (92 days) 1997–2016. Each day is represented by a rectangle. Dense forest (CF): upper panel; open forest (LW): middle panel; lichen hollow (LH): lower panel. See legend below lower panel for temperature distribution from > 0 °C to < −6°C. White rectangles: No data available.

extreme cold and no well-defined frost-free period, with only 14 ± 8 consecutive frost-free days during the growing season. Furthermore, 15.4 ± 3.2 and 6.2 ± 2.4 freeze-thaw cycles repeatedly disturb plant growth in LH and LW, respectively, whereas they rarely occur in CF (1.3 ± 1.4). Severe frost occurs throughout the growing season in LH. High frost intensity prevails in June (−7 to −12 °C), but is still a prominent disturbance factor during the warmest months of the year, both in July (−4 to −6°C) and August (−3.5 to −8.5 °C). Over the 19 years of nocturnal temperature records collected in LH, frost intensity as partitioned in temperature classes below the freezing point prevailed, on average, for 10 days at 0 °C/−2°C, 8–10 days at −2°C/−4°C, 3–10 days at −4/−6°C and 3–8 days at > −6°C. From 1997 to 2016, the rare frost events recorded in CF never reached −2 °C, except on June 13, 2002 when night frost attained −4.4 °C.

Temperature variability The ecological climate of the three ecosystems shows contrasting, large daily temperature variability (maximum and minimum temperatures) throughout the growing season. Temperature range varies greatly from one day to the next according to overcast and clear sky conditions. In July, temperature gradients of up to 17 °C develop in *Cladonia stellaris* mats (9–12 cm thick) under partially cloudy skies, and in excess of 20 °C under clear sky conditions (Kershaw and Field, 1975). The *Cladonia stellaris* mat in mature LW is thermally stratified. This species can survive high temperatures in an air-dried state and can have positive net photosynthesis at thallus

Table 1
Temperature range during frost-free and frost days during the growing season.

	Days with frost	Days without frost
	Lichen hollow (LH)	
Average ± SD	26.5 ± 6.6	15.9 ± 7.0
Maximum	48.7	38.6
	Lichen woodland (LW)	
	Days with frost	Days without frost
Average ± SD	26.1 ± 7.2	17.9 ± 7.4
Maximum	43.6	40.5
	Closed forest (CF)	
	Days with frost	Days without frost
Average ± SD	15.2 ± 6.8	9.2 ± 5.0
Maximum	28.8	27.5

saturation levels as low as 4% (Carstairs and Oechel, 1978). Shade produced by evergreen shrubs protects *Cladonia rangiferina* from extreme heat, even above 40 °C, in sun-exposed parts of LW where *Cladonia stellaris* prevails, given the reduced photosynthetic capacity of lichens at temperatures > 35 °C (Tegler and Kershaw, 1980). *Cladonia mitis* is more xerophytic than other fruticose *Cladonia*, and becomes abundant earlier during postfire succession (see below) than other species.

Temperature magnitudes are far greater during frost days than frost-free days. This is particularly the case in LW and LH, with at least 10 °C greater than in CF, a feature that indicates major energy loss and gain under the influence of clear sky conditions (Table 1). Daily temperature differences ≥ 25 °C occur several times during a season in LW and LH, whereas they seldom exceed 20 °C in CF. The amplitude of diurnal air temperature generally ranges from 10 to 30 °C in LW and LH, and 5–20 °C in CF (Fig. 5). Although mean temperature and mean degree-days (dd, > 0 °C) during the growing season are relatively similar between the three ecosystems (13–15 °C, and 1140–1365 dd), mean minimum and maximum temperatures and dd vary greatly. Mean temperature of the June–August period is 1.6–2.2 °C greater in LW (Table 2). Maximum temperature and dd are progressively higher from CF to LH and LW, an illustration of greater direct radiation reaching the open ground during the day (Langvall and Ottosson-Lofvenius (2002)). In contrast, mean minimum temperature and dd indicate major heat loss in LW and LH during the night compared to CF (Table 2).

Frost occurrence and precipitation Radiative frosts occur during calm, clear sky nights, whereas cloudy and rainy weather reduces or prevents frost-prone conditions. Small precipitation loads during the growing season significantly promote frost frequency in LH (R^2 = 0.45) and LW (R^2 = 0.41). Most frosts occurring in June are associated with precipitation loads totalling ≤120–125 mm (R^2 = 0.54). July and August frosts are associated with monthly precipitation below 175 mm. Given the current spatiotemporal pattern of frost occurrence in the three ecosystems, a warmer climate under a scenario of enhanced summer precipitation and cloudiness would not provide conditions propitious for greater frost frequency during the growing season.

LWs as cold-generating devices – A lichen cover with a high albedo greatly limits the accumulation of energy during the day (Kershaw, 1985; Lafleur and Adams, 1986; Betts and Ball, 1997; Bernier et al., 2011). LW and LH dominated by pale-color lichen covers induce and exacerbate cooling and freezing even in a regional context where the summer climate is usually warm and well above the freezing thresholds that are generally frequent in the fall and winter. Thus, pale-color lichen communities across the boreal biome are very liable to experience frequent and severe frosts during the growing season. Frost origin in these ecosystems is attributable to cold air masses that accumulate under conditions of nocturnal radiative cooling. With the process of energy dissipation due to calm and clear night conditions, a katabatic flow is created (Oke, 1987; Bodine et al., 2009) in lichen ecosystems with a sloping and concave topography, in the form of heavy, cold air masses. The latter masses are thermally stratified and flow downslope by gravity between the scattered trees in LW and fill the topographic LHs. Radiative frost occurs when long-wave radiation dissipated upward by the soil cover during the night exceeds the energy accumulated by the soil during the day. Recurrent radiative frosts in LW and LH occur throughout the eastern boreal forest where the same pattern of vegetation cover is present (Dy and Payette, 2007; Payette et al., 2010; Plasse and Payette, 2015), but, to our knowledge, there are no similar data for the central and western parts of the LW zone. In contrast, open forests and moss-shrub communities thriving on wet soils do not produce radiative frosts because water increases the thermal conductivity of the soil. Wet soils of the boreal environment accumulate more solar energy during the day, and conserve that energy longer during the night, than dry lichen soils (Geiger et al. 2003).

Recurrent radiative frosts negatively affect tree growth, especially in the early part of the growing season in June, i.e., during bud dehardening, when tissues are sensitive to frost stress, which causes severe damage due to ice formation in plant cells. Spring frosts kill needles, dehardening buds, and newly formed shoots (Sutinen et al., 2001; Bigras et al., 2004). Also, death of terminal buds can lead to reiterative growth that subsequently affects tree architecture (Bégin and Filion, 1999). Multiple radiative frosts over a short period create an accumulation of stress, resulting in reduced tree germination, stem anomalies, and increased seedling and sapling mortality (Sakai and Larcher, 1987; Inouye, 2000; Hawkins et al., 2003; Coop and Givnish, 2007), especially in LW (Dy and Payette, 2007; Plasse and Payette, 2015).

4. Postfire succession in lichen woodlands

Most LWs are postfire plant communities of various ages, although there are exceptions in northernmost fire-free treeline sites (Vézeau and Payette, 2016). Postfire lichen and bryophyte succession in LWs follows a general progression (Fig. 6) described by Ahti (1959), Bergerud (1971), Maikawa and Kershaw (1976), Carroll and Bliss (1982), Auclair (1983), Foster (1985), Morneau and Payette (1989), Payette (1992) and Girard et al. (2017). Species growing in old LW stands are present in the first years after fire, a pattern found in most fire-prone lichen communities (Johnson, 1981; Morneau and Payette, 1989). After initial establishment during the first two decades after fire, further changes in vegetation development are associated with species abundance (Johnson, 1981; Morneau and Payette, 1989). Recovery of vegetation after fire is by vegetative multiplication from below-ground organs (rhizomes, lignotubers, etc.) and propagules (seeds, spores, lichen thallus fragments, etc.) (Flinn and Wein, 1977, 1988). Buried viable seeds are said to play little role in the recovery process of postfire LWs (Johnson, 1975).

Maikawa and Kershaw (1976) and Kershaw (1977) have identified four stages of postfire succession, with the closed-crown black spruce-feathermoss forest as the final stage (Fig. 6). The first stage, from year 1 to year 20, is dominated by *Polytrichum piliferum* Hedw., *Ceratodon purpureus* (Hedw.) Brid.), *Trapeliopsis granulosa* (Hoffm.) Lumbsch. and *Placynthiella oligotropha* (J. R. Laundon) Coppins & James, and several cup, horn and trumpet *Cladonia*. *Cladonia mitis* is the dominant lichen in 30 year-old LWs, such as those in western and eastern Canada (Black and Bliss, 1978; Foster, 1985; Morneau and Payette, 1989; Sirois and Payette, 1989). From year 20 to about year 60, the ground flora is represented by *Cladonia stellaris* and *Cladonia uncialis* (L.) F. H. Wigg., whereas black spruce and *Stereocaulon paschale* form the third stage, from year 60 to about year 130. The spruce-moss forest replaces the spruce LW after year 130.

In contrast, in northern Saskatchewan, *Cladonia stellaris* achieves dominance in LWs > 100–120 years (Scotter, 1964). The ground flora of jack pine LW of northern Saskatchewan and Alberta is dominated by *Cladonia mitis*, regardless of the postfire age of the stands (Skatter et al., 2014), between the pioneer stage of *Polytrichum* sp., *Cladonia coccifera* (L.) Willd., *Cladonia cristatella* Tuck., *CLadonia deformis* (L.) Hoffm., *Cladonia sulphurina* (Michx.) Fr. and *Cladonia gracilis* (L.) Willd. and

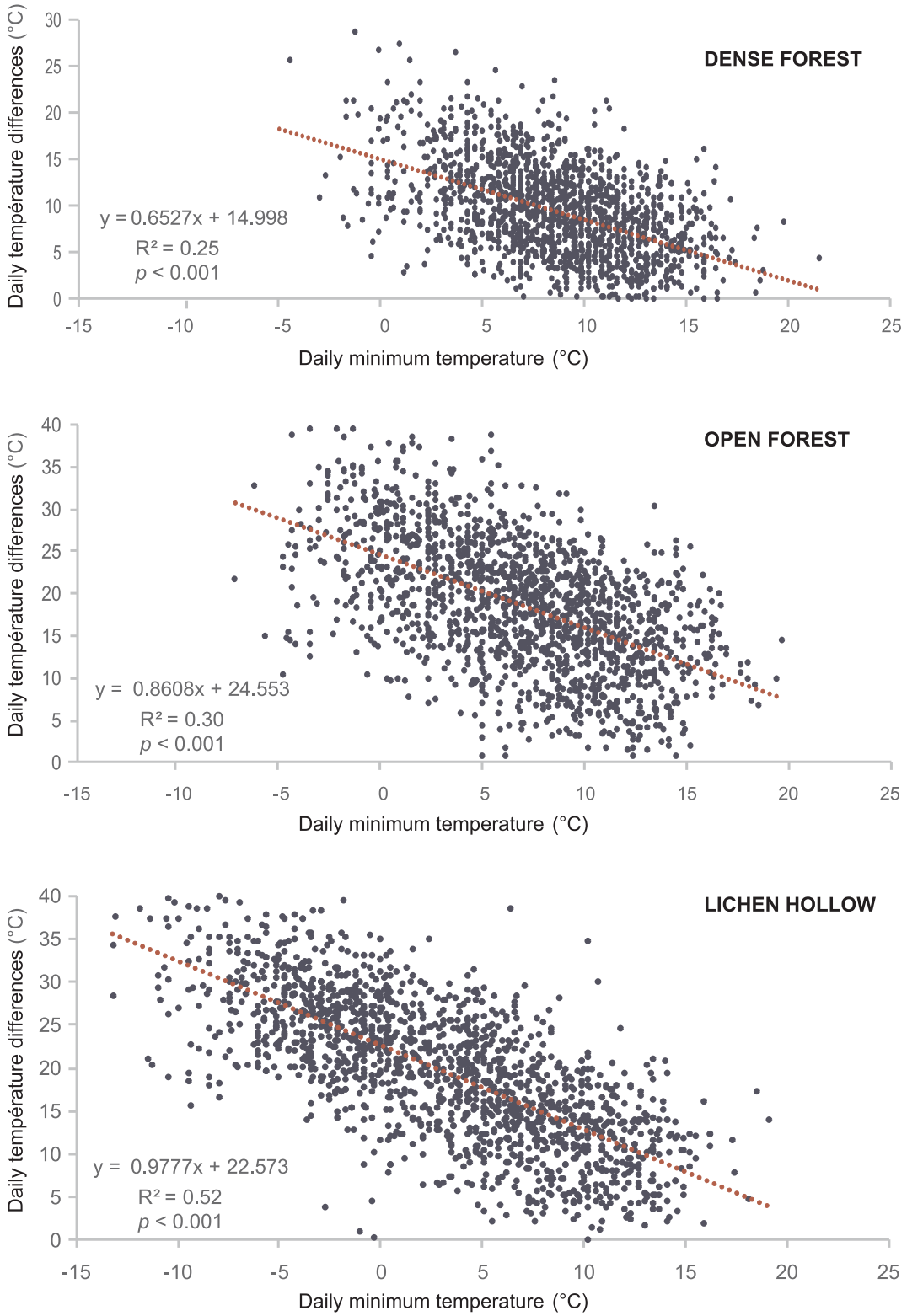

Fig. 5. Diurnal air temperature range during the June–August growing season (92 days) 1997–2015, inclusively. Each daily temperature difference (Y axis) is calculated by subtracting maximum temperature of day *t* from minimum temperature of day *t* + 1. Dense forest: upper panel; lichen woodland : middle panel; lichen hollow: lower panel.

year 80. *Stereocaulon paschale* is rare if not absent in most of the stands. Mat-forming species of *Cladonia* are prolific in 80–100 year-old stands in lodgepole pine LW of western Canada (Sulyma and Coxson, 2001). In British Columbia, the ground vegetation of 100–130 year-old pine LWs is occupied by *Cladonia mitis* and *Cladonia rangiferina* mats. The > 60 year-old *Picea-Stereocaulon* phase of Maikawa and Kershaw (1976) is absent in the Carroll and Bliss (1982) sites of northern Saskatchewan and northeastern Alberta. Further, during succession in > 80 year-old stands, *Cladonia stellaris*, *Cladonia rangiferina* and several bryophytes achieve higher cover. The ground cover of the first 20 years of postfire succession in southeastern Labrador is dominated by *Polytrichum juniperinum* Hedw. and *Trapeliopsis granulosa*, and several cup, horn and

Table 2
Mean temperature variability (± SD) and mean degree-day variability (± SD) during the growing season (June–August).

Vegetation cover	Max. T°C	Mean T°C	Min. T°C	Max. degree-days	Mean degree-days	Min. degree-days
Lichen hollow (LH)	22.8 ± 5.5	13.3 ± 3.7	3.1 ± 6.1	2040 ± 159	1204 ± 70	294 ± 100
Lichen woodland (LW)	25.4 ± 6.4	15 ± 3.7	6.9 ± 4.8	2314 ± 119	1365 ± 51	624 ± 74
Closed forest (CF)	18 ± 4.4	13.1 ± 3.4	8.7 ± 3.8	1571 ± 203	1140 ± 141	759 ± 109

trumpet *Cladonia* (Foster, 1985). Then, pioneer species are replaced by *Cladonia mitis*, which persists for 40–60 years. Eighty to 90 years after fire, the mat cover of *Cladonia stellaris* reaches a maximum of 50–75%. Thereafter, this species remains dominant until the next fire occurs. Most postfire LW chronosequences in subarctic Quebec follow the same seral pattern. Extensive *Cladonia stellaris* mats occupy the ground vegetation of old growth LWs (Hustich, 1951; Rencz and Auclair, 1978; Auclair, 1985; Morneau and Payette, 1989). Lichen biomass increases with postfire stand age, from 530 kg ha^{-1} in stands < 30 years to 8010 kg ha^{-1} in LW stands > 90 years (Arseneault et al., 1997), and in sites with high precipitation loads (Crête et al., 1990). In jack pine LW of Saskatchewan, however, Skatter et al. (2014) indicate that young stands (21–30 years old) produce a larger cover of lichen forage than stands 50–90 years old. Ahti (1959) relates the dominance of *Cladonia stellaris* in LW to the relative growth rates of the lichen species involved in the successional process. Horn, cup and trumpet *Cladonia* abundant during the early postfire stages of succession grow faster than the *Cladinae*, which therefore achieve dominance at a later stage. According to Ahti (1959), *Cladonia stellaris* develops at the slowest rate and, hence, is the final dominant of the successional process.

In sandy LW sites disturbed by wind action, vegetation recovery follows roughly the same chronosequential pattern as in postfire LW chronosequences of northern Quebec and Labrador, except that bare sands, the first pioneer stage, is colonized by *Polytrichum piliferum*, subsequently followed by *Stereocaulon paschale* and *Racomitrium canescens* (Hedw.) Brid. (Filion and Payette, 1989). At stage 2, the moss *Racomitrium* forms an extensive mat that is occupied progressively by *Steteocaulon* and several invading vascular and cryptogamic species. Although it is not possible to assign a specific age to most developmental stages during posteolian chronosequences, further succession as evidenced by increased podzolic soil development shows the replacement of *Stereocaulon* by *Cladonia mitis*. With time, in older posteolian LWs, *Cladonia stellaris* becomes the dominant species to the detriment of *Cladonia mitis* (Fig. 6).

As indicated earlier, postfire LW chronosequences in the Northwest Territories (the Abitau-Dunvegan Lake area) differ from those of western, central and eastern Canada. *Stereocaulon paschale* woodlands replace *Cladonia stellaris* woodlands in a more or less continuous zone from west of Churchill to Great Slave Lake, immediately north and south of 60°N, and cover 2600 km^2 (Kershaw, 1977). Both *Stereocaulon* and *Cladonia stellaris* LW are typical of sandy soils and represent the final recovery phase after fire (Kershaw, 1977). It is not clear what particular combination of environmental and edaphic factors controls each of these LWs. According to Kershaw and colleagues (Maikawa and Kershaw, 1976; Kershaw, 1978; Kershaw and Smith, 1978), the *Stereocaulon paschale* phase during the recovery of LWs develops 60–80 years after fire. In contrast with posteolian LW chronosequences (Filion and Payette, 1989), the delayed entry of *Stereocaulon paschale* in the successional process would reflect its extreme sensitivity to thermal stress (> 35 °C) with the gradual accumulation of an organic layer and enhanced retention of moisture over the initial 60 years of succession (Kershaw and Smith, 1978). The slow development of *Stereocaulon paschale* cover is thought to be correlated to the extreme surface microclimate of burned woodlands at this latitude (60°N). In addition of the physiological hypothesis of Kershaw and colleagues and Johnson's view (1981) that the abundance of the species is best explained by habitat requirements, others researchers (Ritchie, 1959; Brown and Mikola, 1974) have argued that the *Stereocaulon* phase is closely associated with excessive grazing by caribou (or reindeer, *Rangifer tarandus*, Linnaeus 1758). This view suggests that *Stereocaulon paschale* is a

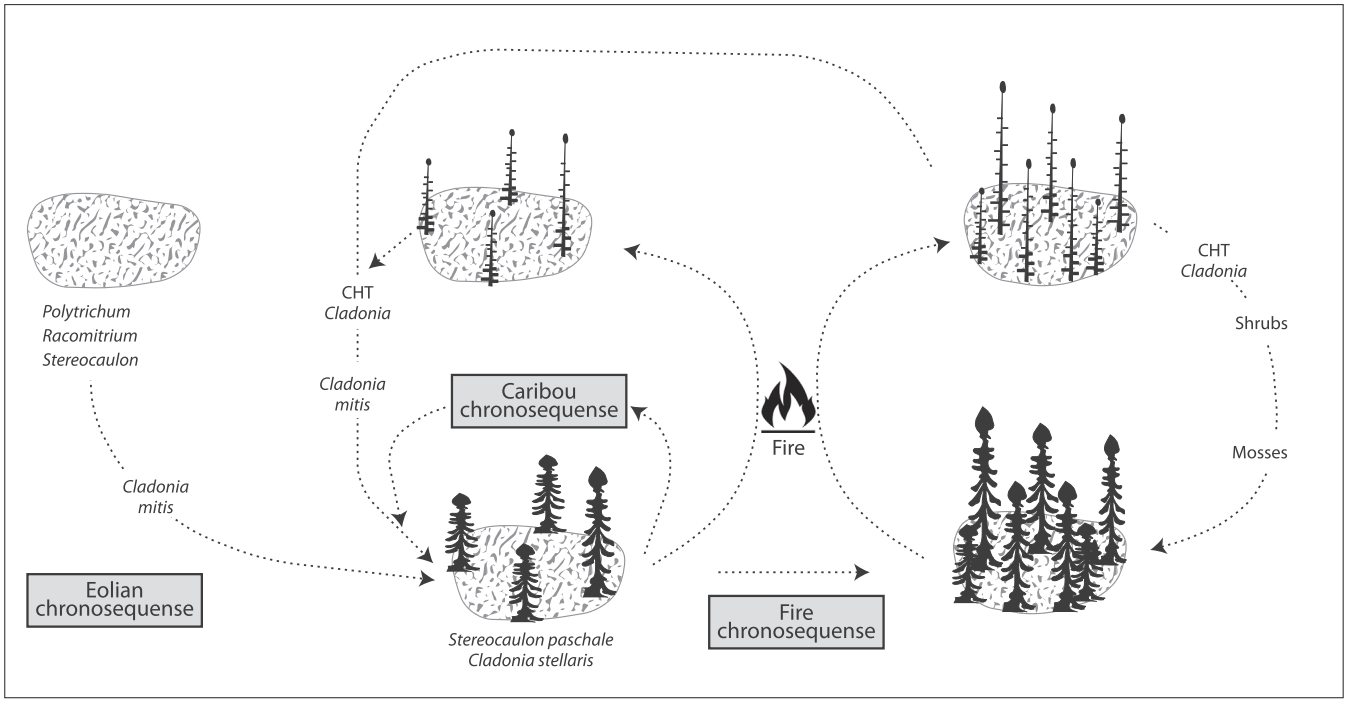

Fig. 6. Schematic successional trajectories of postfire, posteolian and postcaribou trampling chronosequences of lichen woodlands and moss forests.

pioneer species and the first site colonizer after fire and heavy grazing. In Finnish alpine heaths, reindeer avoid *Stereocaulon paschale* or graze it less than *Cladinae*, thus explaining why the species is abundant in overgrazed lichen grounds (Stenroos et al., 2016). Posteolian chronosequences in eastern Canada also show *Stereocaulon* as a pioneer, postdisturbance species (Filion and Payette, 1989), even forming posteolian *Stereocaulon*-white spruce LWs, whose local dominance is associated with saltation of fine sand (Fig. 3).

Whether LW is a climax forest or a pioneer stage in a succession leading to the closed-canopy feathermoss boreal forest has been much debated (Hustich, 1951, 1957; Maikawa and Kershaw, 1976; Kershaw and Rouse, 1976; Foster 1985) (Fig. 6). According to Kershaw (1977) and Sulyma and Coxson (2001), without the influence of fire, LWs would develop a closed-crown canopy with the extirpation of the lichen mats (Kershaw, 1977). Although Kershaw (1977) shared this view, he did agree that field evidence supporting such a conclusion was lacking. Indeed, such a shift event is rare, and the dominance of LW in the northern part of the boreal biome is evidence of the long-term maintenance of this ecosystem regardless of the fire regime (Payette et al., 2001). The long-term residency of LWs in well-drained podzolic soils near the Arctic treeline has been validated by radiocarbon dating of soil charcoal and forest peat (Payette and Morneau, 1993; Payette et al., 2008; Auger and Payette, 2010; Vézeau and Payette, 2016).

Postfire tree establishment – The initial period of postfire regeneration is critical for future LW development, and several structural characteristics of LW are determined during this period (Black and Bliss, 1980; Cogbill, 1985; Morneau and Payette, 1989; Sirois and Payette, 1989; Sirois, 1992, 1993; Riverin and Gagnon, 1996; Sirois, 1995). Germination of tree seeds and seedling survival rates during the early phase of forest development are influenced by soil pH, ash toxicity, temperature, water availability, and nutrient content (Black and Bliss, 1980; Dyrness and Norum, 1983; Dyrness et al., 1989). Scattered seedling establishment generally occurs during the first years after fire. The number of established postfire trees rarely exceeds the number of prefire mature trees (Jayen et al., 2006; Johnstone and Chapin, 2006). Seedling survival varies greatly according to local factors such as low fire severity, successive stand disturbances during a short period of time, and soil moisture (Jasinski and Payette, 2005; Johnstone and Chapin, 2006; Johnson, 2007; Girard et al., 2009; Veilleux-Nolin and Payette, 2012). Rarity of *Sphagnum* substrates (Veilleux-Nolin and Payette, 2012; Boiffin and Munson, 2013) and other types of moist ground (Johnson, 2007) in postfire LWs greatly limits successful establishment and survival of spruce seedlings.

The two principal tree species of LW are well adapted to fire because of serotinous (jack pine) and semi-serotinous (black spruce) cones that act as effective aerial seed banks and disperse the seeds immediately and many years after fire, respectively. Heat induces cone opening, and seed dispersal becomes important immediately after fire and then decreases significantly as time passes (Wilton, 1963). Cones are still dispersing seeds 8–20 years after fire (Wein, 1975; Viereck, 1983). Seed dispersal decreases rapidly after fire, and lichen expansion reduces spruce germination and growth (Brown and Mikola, 1974; Kershaw, 1977). Seed viability over time follows the same trend as four years after fire, when only 2–15% of the seeds in standing cones are still viable, although a small number of viable seeds may be found in 15–20 year old cones (Vincent, 1965; Zasada, 1971). The overall regeneration pattern of black spruce is also dependent on seedling mortality during the first 5–10 years following fire due to soil moisture deficit and thermal stress (Duchesne and Sirois, 1995; Lavoie and Sirois, 1998; Kemball et al., 2006; Moss and Hermanutz, 2009). Indeed, in the early recovery phase, limited soil moisture with very high surface temperatures and large diurnal temperature fluctuations reduce seedling survival (Veilleux-Nolin and Payette, 2012). According to Kershaw (1977), the extreme microclimate of burnt surfaces is responsible for the long delay in the development of a mature lichen surface. Temperatures in excess of 45 °C for several hours prevail on recently burnt surfaces (Kershaw, 1978). Seedling establishment occurs in a short period of time, indicating that stand density depends on regeneration conditions, including seed input and seedbed quality, soon after the fire. Scarcity of young postfire individuals suggests that seedling recruitment becomes a rare event as the lichen mat thickens. After the early postfire stage, most regeneration is by layering from spruce trees established from seeds (Morneau and Payette, 1989). Thick lichen mats are important barriers to spruce establishment (Kershaw, 1977) and, in contrast, polygonal fissures along desiccated mats are favourable sites for seedling establishment in mature LWs (Cowles, 1982; Filion and Payette, 1989; Houle and Filion, 2003). Among other factors influencing tree survival in LW, slugs (molluscs) and small rodents are the most important predators of black spruce seeds and seedlings, particularly in recent burns, which may influence tree regeneration in these sites (Côté et al., 2003, 2005).

Based on cross-dating of black spruce hypocotyls (stem sections below ground level, in thick organic layers facilitating the production of adventitious roots), St-Pierre et al. (1992) and DesRochers and Gagnon (1997) demonstrated that the regeneration window is mostly restricted to the first years after fire. However, tree establishment in several LWs may occur during the first two decades after fire, before the development of the full lichen carpet (Brown and Mikola, 1974; Kershaw, 1977), probably because of dispersal from seed-bearing trees surrounding burned woodlands (Payette et al., 2000). Also, burial of the stem base during succession is rather superficial in LW sites, with its thin organic layer recurrently impacted by fire. Shallow burial of stems in these LWs (Sirois and Payette, 1989) allows relatively accurate dating of postfire seedlings based on growth ring counts from a stem base free of adventitious roots, which suggests a regeneration window sometimes longer than the < 5-year window often proposed (DesRochers and Gagnon, 1997).

According to Larsen (1980) and Cowles (1982), woodland lichens inhibit seed germination, and even reduce tree growth. Several factors may be involved in the overall negative effect that lichens have on seed germination and seedling emergence and establishment, such as allelopathy (Arsenault, 1979), altered soil temperature, and light attenuation (Zamfir, 2000). The predominant distribution of spruce seedlings at the margin of lichen polygons (Cowles,1982; Filion and Payette, 1989; Sirois, 1992, 1993; Houle and Filion, 2003; Johnson, 2007) is indirect evidence that thick lichen mats act as a physical barrier against tree establishment. Lichen removal increases white spruce establishment but reduces growth in juvenile spruce > 20 cm in height (Houle and Filion, 2003). On the other hand, Cowles (1982) has argued that lichens produce an overall beneficial effect on spruce tree growth, due to increased soil water retention capacity and nutrient leaching from the decomposing lower portion of the lichen mat.

Differential tree growth in LW Tree growth varies greatly in LW according to the type of soil cover during postfire succession. The rates of height growth of spruce seedlings established immediately after fire are always higher than those of seedlings established on lichen mats several decades later (Fig. 7) (Plasse and Payette, 2015). The growth of the postfire cohort is unaffected by the cooling effect of the lichen cover because their early growth period is under different soil conditions dominated by blackened soil surfaces (lower albedo) that remained free of lichens, at least during the first decade after fire (Veilleux-Nolin and Payette, 2012; Boiffin and Munson, 2013). Height growth of seedlings established later in successional stages, particularly from seed-bearers of the postfire cohort, is reduced because of the cooling and radiative nocturnal frost-prone effect of extensive covers of pale *Cladinae*. Frequent frost occurrences early in the growing season in mature LWs often kill the apical bud of seedlings and saplings, thus reducing the rate of vertical stem growth and producing multi-stemmed individuals. According to Plasse and Payette (2015), the low rates of height growth of LW and LH spruce established on pale lichen mats vary between 1.1 and 3.1 cm $year^{-1}$ (Fig. 7).

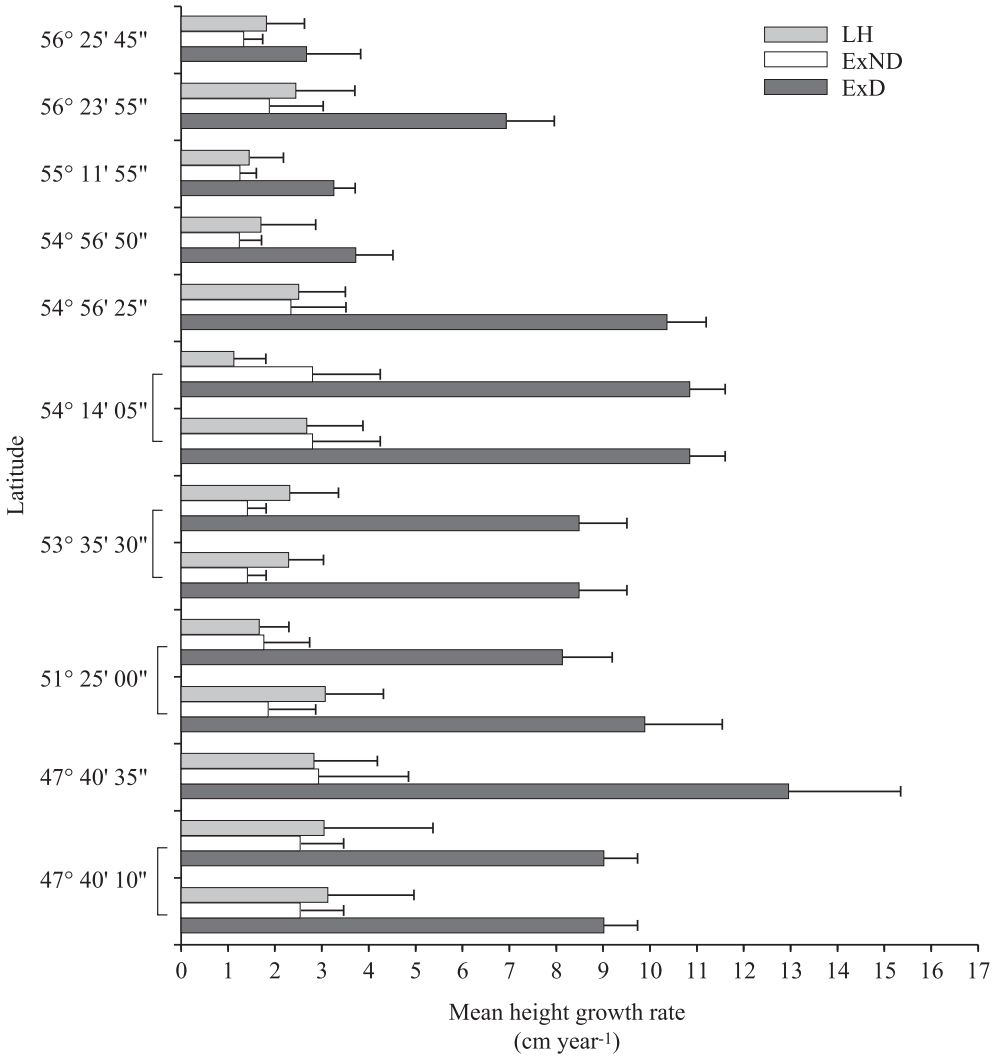

Fig. 7. Mean height growth rate of LH spruce, early-established (ExD, growing on darkened soil surface) and late-established (ExND, growing on pale-color lichen carpet) postfire spruce according to latitude (according to Plasse and Payette, 2015, Journal of Ecology).

5. Caribou and lichen woodlands

Barren-ground caribou undertake seasonal migrations between the Arctic to the boreal forest. LW is home to most large herds of migratory and woodland caribou, particularly in winter, when fruticose *Cladonia* are among their preferred forages. Demographic growth and decline of caribou herds has occurred repeatedly over the last centuries (Bergerud, 1988; Messier et al., 1988, Morneau and Payette, 2000; Payette et al., 2004; Vors and Boyce, 2009). The increasing numbers of caribou during a demographic growth stage leave lichen grounds of LWs heavily disturbed by trampling and grazing, and the thalli of fruticose *Cladonia* broken into a multitude of tiny fragments when dry (Pegau, 1970; Boudreau and Payette, 2004b). During a peak of caribou abundance (as in the late 1980s and early 1990s in northeastern Quebec-Labrador), the lichen cover is almost entirely destroyed and converted into barren mineral and organic substrates over thousands of km^2 (Morneau, 1999) (Fig. 8). Between 1989 and 1992, caribou numbers in this area exceeded the numbers supported by the annual production of lichen biomass, probably as a result of excessive trampling in feeding areas (Arseneault et al., 1997; Morneau, 1999). During this period, the large caribou population caused lichen depletion in the animal's calving grounds and winter habitat (Morneau, 1999).

Declining abundance of caribou favors the return of lichens through successional trajectories similar to those of postfire chronosequences (Fig. 6). Destruction of fruticose *Cladonia* mats allows other species of lichens (crustose lichens, and cup, trumpet and horn *Cladonia*) to establish and expand, especially on the most disturbed sites where barren soils are exposed by heavy trampling (Boudreau and Payette, 2004b). Also, a collateral effect of excessive trampling is the establishment of conifer seedlings on bare mineral soils during years following high caribou activity (Dufour-Tremblay and Boudreau, 2011). Lichen recovery is faster in mature LWs impacted by light to moderate trampling, where budding of podetial fragments of *Cladonia stellaris* (Yarranton, 1975) favors clone enlargement. Reconstruction of lichen mats by clonal fusion accelerates the development of LW grounds so that they come to resemble those present prior to caribou disturbance. Fused podetial fragments of mat-forming *Cladonia* regenerate successfully provided trampling does not reoccur repeatedly. Consequently, disturbance of the lichen carpet by caribou induces complex successional pathways in the sense that repeated over-grazing can change the course of succession (Boudreau and Payette, 2004b).

Periods of caribou activity in LW are recorded by trampling scars produced by caribou hooves. Trampling scars formed on tree roots and low branches crossing caribou trails are dated by tree-ring counts (Morneau and Payette, 1998). Changing caribou activity revealed by the number of trampling scars produced per year over a large area provides information on migration routes of the animal and its impact on vegetation through time. Periods of high caribou activity in Quebec-

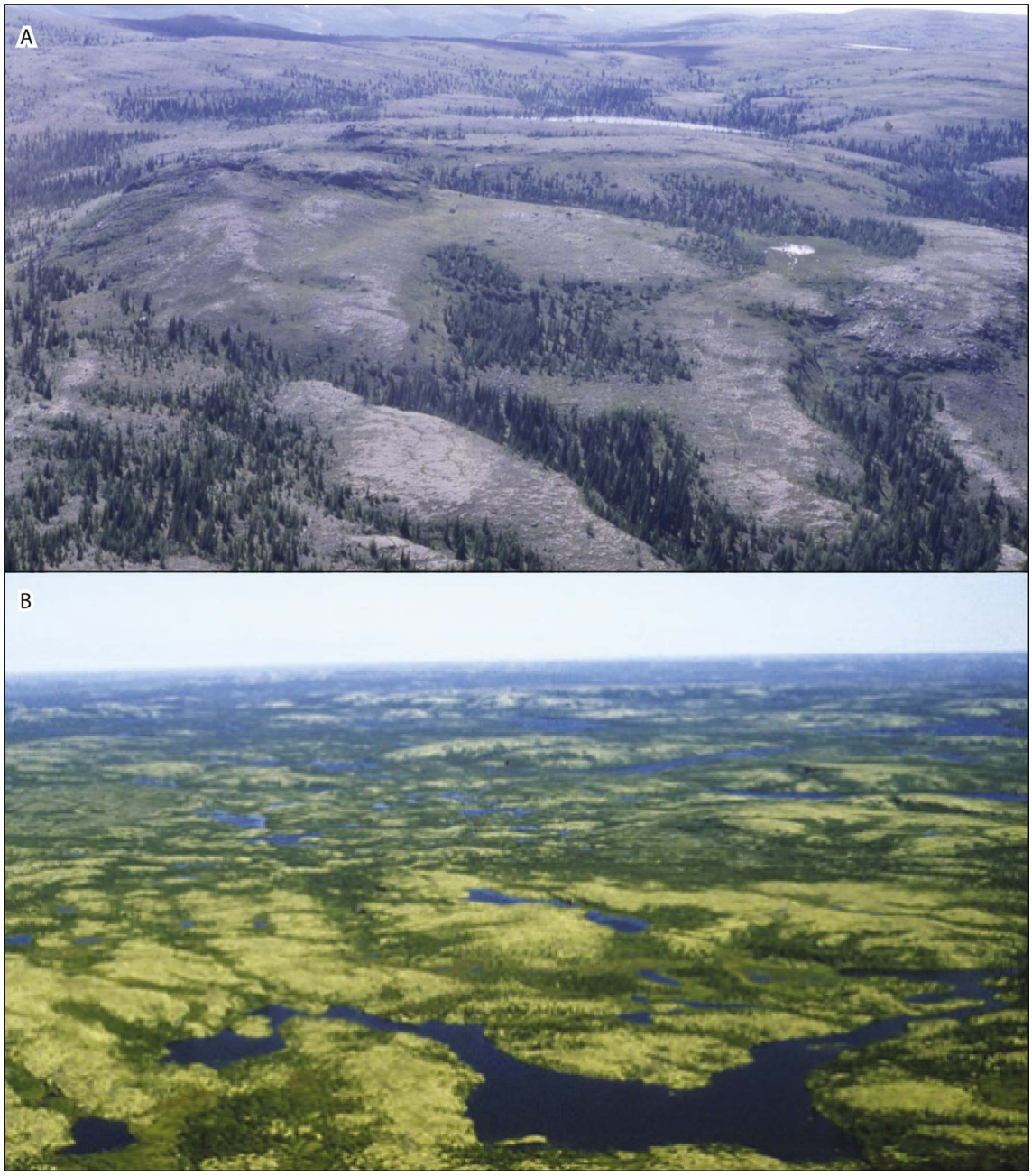

Fig. 8. (A) «Delichenized» lichen woodlands caused by heavy trampling and grazing of migratory caribou during a population peak of the late 1980s and early 1990s in northeastern Quebec-Labrador. The lichen cover is destroyed and converted into barren mineral and organic substrates over thousands of km^2 in comparison to (B) untouched lichen woodlands.

Labrador occurred at an interval of 100 years from the late 18th to the late 19th century, and in the late 20th century (Payette et al., 2004). In the Northwest Territories, Zalatan et al. (2006) also used the age-frequency distribution of trampling scars to document migration routes of the Bathurst and Beverly caribou herds. Similar spatiotemporal patterns of caribou activity between the two groups of sites have been documented for the period between 1760 and 2000. Caribou activity was high during the mid-1940s and 1990s, and very low during the 1920s, 1950s–1970s and at the turn of the 21st century. Caribou activity reported by Zalatan et al. (2006) is located in the *Stereocaulon* LW area (see section on postfire succession above) previously studied by Maikawa and Kershaw (1976). Whether the dominance of *Stereocaulon* in mature LWs is associated with fire disturbance or caribou activity, as suggested by Ritchie (1959) and documented by Zalatan et al. (2006), remains open to interpretation and consequently deserves further study.

6. Origin of the lichen woodland

The origin of LW is polygenetic, and its “life history” spans an important part of the Holocene period. Whether LW was the first tree community to establish on deglaciated terrain of the Precambrian Shield remains unknown, but LWs grow almost exclusively in this type of geosystem. Pollen grains and macrofossils are biological indicators commonly used to reconstruct past vegetation development and changes caused by climate and disturbance events during the Holocene (Ritchie, 1987; Birks, 2003). However, the peculiar nature of LW, with dominant lichens and scattered vascular plants, makes it difficult to identify periods of past inception and expansion from fossil remains buried in sedimentary environments. Therefore, to address the origin and spatiotemporal distribution of LW, it is best to use indirect evidence from the main resident tree species, black spruce, i.e., spruce pollen profiles constructed from lake and peat deposits (Asselin and Payette,

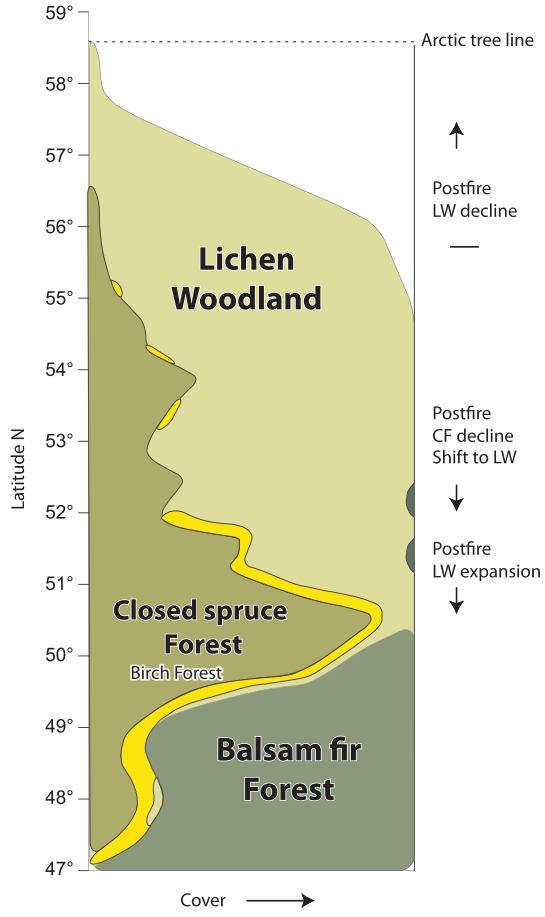

Fig. 9. Distribution of LW and other main forest types of the boreal forest according to latitude. Data according to Payette et al. (2001), Girard et al. (2008), Pollock and Payette (2010), and this study. Southward expansion of LWs at the expense of closed-crown spruce forests. Extirpation of LWs in the forest-tundra zone northward to the Arctic tree line. Distribution of postfire paper birch forests from the southern boreal forest to the northern part of the LW zone.

2005a). Compared to the present climatic and biogeographical context of LW development, early- and mid-Holocene times were warmer and more humid (Ritchie, 1987; Engstrom and Hansen, 1985; Lamb, 1985; Gajewski et al., 1993; Richard, 1995). Shortly after deglaciation of northernmost Quebec and Labrador about 6000 years ago, spruce and shrub pollen influxes were twice those of modern values (Gajewski et al., 1993), suggesting a denser forest cover and absence of LW (Richard, 1995). Asselin and Payette (2005a) proposed that the opening of the boreal forest and correlative expansion of LW based on declining abundance of spruce pollen began about 3000 cal. years ago, and intensified during the last thousand years (Gajewski et al., 1996). Thus, landscape opening and LW inception, at least in eastern Canada, likely occurred during the late Holocene (Gajewski et al., 1993; Asselin and Payette, 2005a), with wildfire as the principal triggering mechanism (Asselin and Payette, 2005a).

To our knowledge, the inception and expansion of LWs during the late Holocene occurred at the expense of closed-crown forests in a southward trend from the present forest-tundra and LW zones to the closed-crown forest zone (Fig. 9) (Pollock and Payette, 2010). The process by which closed-crown forest shifted to become LW has been documented for several sites that show different sets of causal factors acting in synergy (Payette et al., 2000; Payette and Delwaide, 2003; Jasinski and Payette, 2005; Girard et al., 2008, 2009, 2011; Côté et al., 2013). The creation of LWs in the northern part of the boreal forest, corresponding to the LW zone proper, where they represent the main forest type on well-drained soils, is due to failure of postfire regeneration. Recurrent fires at short intervals and light fires that maintained thick darkened organic layers appear to be the proximal factors involved in the shifting process. The number of seedling niches in these sites is largely reduced by the absence of moist ground, in particular *Sphagnum* substrates, which provide one of the best seedbeds (Veilleux-Nolin and Payette, 2012; Boiffin and Munson, 2013).

According to current evidence of the dual distribution of LWs and closed-crown forests in eastern Canada, the LW zone is expanding southward into the closed-crown forest zone. The shifting process is currently very active even in the closed-crown forest zone, where superimposed (compound) disturbances associated with insect epidemics followed by small to extensive fires are transforming dense forest stands to LWs (Fig. 6) (Payette et al., 2000; Jasinski and Payette, 2005). Furthermore, the southernmost LWs in eastern Canada were created in the late Holocene, at least 1500 years ago. Over the last 50–60 years, 9% of the area covered by the closed-crown forest zone in southcentral Quebec has shifted to LW (Girard et al., 2008), a major reduction in forest cover caused by local fire and biotic disturbances, not climate. Elsewhere in the mixed boreal forest of western North America, variations in fire severity as in LWs have also changed the course of postfire succession from conifer to mixed and deciduous stands (Johnstone and Kasischke, 2005). A similar pattern exists in eastern Canada showing the patchy distribution of postfire deciduous forests dominated by paper birch from the southern boreal forest to the northern part of the LW zone (Fig. 8). Several paper birch forests are forming an intermediate postfire stage (Foster and King 1986) toward a late postfire stage composed of mixed forests dominated by balsam fir (Couillard et al. 2012).

While LWs are currently expanding in the southern part of the boreal biome, postfire extirpation of trees in the northern part of boreal forest, the forest-tundra zone and to a minor extent in the LW zone proper, is causing large-scale deforestation (Figs. 9 and 10). Fire-induced deforestation can follow either of two modes of operation. The first mode is associated with lichen krummholz stands (shrubby LWs, Fig. 3) and marginal LWs at the Arctic treeline that show a low regenerative potential rapidly eradicated after a single fire event (Fig. 10) (Arseneault and Payette, 1992, 1997; Asselin and Payette, 2005b; Payette et al., 2008). The long-term maintenance and stability of these communities during the Holocene was probably due to low fire frequency, particularly for large fires, and by continuous vegetative multiplication by layering. The systematic deforestation of northernmost LWs over the last millennium and their transformation into lichen tundra communities (Arseneault and Payette, 1992; Asselin and Payette, 2005b; Payette et al., 2008) has produced a neat negative feedback resulting in a sharp decrease of fire size and frequency due to reduced combustible fuel. This large-scale deforestation process has resulted in the preservation of isolated, relict, old-growth LWs (Fig. 11).

The second mode of deforestation occurs mostly in the southern part of the forest-tundra and in the LW zone where spruce generally has an arborescent growth form with a higher seed-production potential. Here, successive depletion of tree populations by recurrent fires progressively decreases the regenerative potential of black spruce populations, probably exacerbated by declining surfaces of moist seedbeds. Sustained depletion of tree populations following several fires was a key process in the development of the forest-tundra zone (Payette and Gagnon, 1985). For example, large fires during the 1950s in northern Quebec significantly reduced the density of LW spruce populations on uplands but not in lowlands (Sirois and Payette, 1991). Complete exclusion of tree populations by fire occurred in 43% of upland sites of the forest-tundra, resulting in the patchy distribution of LWs typical of this biogeographical zone. The ecological impact of the fires of the 1950s contributed to the southward expansion of the forest-tundra into the section of the upper boreal forest corresponding to the LW zone. The proportion of stunted spruce trees in 1950s postfire populations was often more important than in prefire populations on the same sites, suggesting more rigorous growth conditions following tree removal and

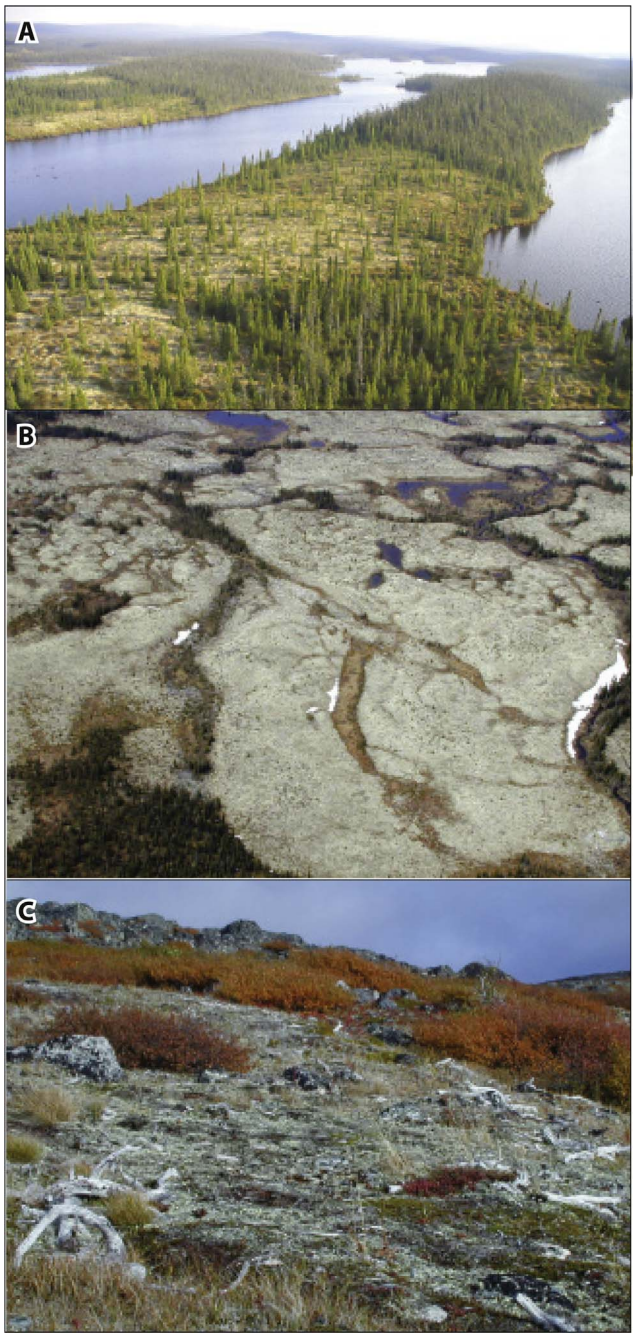

Fig. 10. One-shot postfire shift of (A) closed forest to lichen woodland in the closed-spruce forest zone, (B) lichen woodland to lichen parkland in the forest-tundra zone and (C) shrubby lichen woodland (krummholz) to lichen tundra at the Arctic tree line.

forest opening (Sirois and Payette, 1989). Tree removal by fire induces significant changes in wind, temperature and snow conditions (Rouse and Kershaw, 1971; Rouse, 1976; Arseneault and Sirois, 1990), producing a colder environment for tree establishment, survival and growth. Depauperate LWs are maintained as lichen parklands where the more exposed lichen ground exacerbates the negative climatic impact of snow-drifted surfaces on tree growth-form degradation, which may become an additional causal factor of future fire-induced deforestation. In contrast to this major transformation of the forest environment, minor advances of northern limit of LW (Lavoie and Payette 1994) and increase in tree establishment due to recent warming are currently underway at the Arctic treeline in eastern Canada, but no data are presently available to document and validate the magnitude of this trend.

7. Conclusion

The open structure and botanical composition of LWs determine many of their attributes and functions. No other lichen-dominated tree ecosystem occupies such a continent-wide distribution in the northern hemisphere, not even in the larger Eurasia, where climatic conditions are favorable for LW development. The extensive well-drained, acidic and nutrient-poor podzolic soils of the Canadian Precambrian Shield in subarctic Canada provide the ideal environmental conditions for its growth, maintenance and expansion. LW is a dynamic ecosystem in the face of the heavily disturbance-prone subarctic environments where changing climate, fire and caribou disturbances are the main driving factors influencing its long-term dynamics. Initiation and expansion of LWs most likely occurred when warmer, humid climatic conditions gradually subsided during the late Holocene, with wildfire as the medium driving the expansion and contraction of the system.

Deforestation of the forest-tundra zone has occurred over the last thousand years. Despite prevailing climatic warming since the end of the Little Ice Age (Grove, 2004), several LWs near the Arctic tree line have shifted to lichen-tundra communities. While LWs are unable to transgress the tree line into the proximal Arctic tundra, they are currently expanding within the closed-crown boreal forest. LW expansion in the southern boreal forest appears independent of climate, whereas the severity of fire seems to be the factor influencing the shift from dense to depauperate tree populations. LWs are also agents of climatic cooling within the boreal forest matrix. Several climate models suggest positive feedback from the expanding boreal forest toward northern latitudes and climatic warming. Boreal forests affect the climate by decreasing surface albedo and increasing carbon sequestration. However, models predicting warming with increasing vegetation cover consider the boreal forest as a homogeneous dense forest irrespective of its structure (Bonan et al., 1992; Foley et al., 1994). Because the forest landscape is a mosaic of different ecosystems with variable radiative forcing, the magnitude of the climatic impact of the boreal forest remains unknown (Scheffer et al. 2012). As we have shown, LW exerts a negative climatic impact on the environment, in particular the greater albedo of dry-pale lichen covers in summer and the open structure, which decreases the greenhouse effect, resulting in a reduction of the frost-free season and an increase in frost events. The current increase in LW cover associated with fire disturbance creates propitious conditions for greater cooling and frost events. Models predicting future changes in climate may take into consideration the cooling window of deforested environments in contrast to the warming window of dense forests (Bala et al., 2007). Periods of increased frost frequency caused by long-lasting dry, clear sky conditions coincide with periods of multiple forest fires (Plasse and Payette 2015).

Recent evidence shows that several sectors of the closed-crown forest zone are presently in a process of dramatic change driven by fire disturbance that will eventually see them transformed to northern woodlands (Girard et al., 2008). Projections of the future boreal climate suggest an increased probability of forest fires (Flannigan et al., 2000). Any prevalence of dry conditions will promote fire events and possible failure of tree regeneration in dry to mesic closed-crown forest stands. If the current biogeographic trend from dense to open forests continues, it will more likely cause negative climatic feedback through the creation and extension of lichen-dominated ecosystems. Future spatially explicit climate models should take into consideration the potential negative impact of lichen-dominated ecosystems across the boreal zone. In contrast, any future expansion and successional maintenance of LWs caused by fire becomes a positive asset for migratory caribou herds, contrary to recent views on this topic (Sharma et al., 2009).

In terms of ecosystem management, there are concerns about the maintenance of the southernmost LWs within the closed-crown forest zone as poor carbon sinks (Gonzalez et al., 2013; Tremblay et al., 2013; Dufour et al., 2016). Projects involving LW plantation sites in the closed-crown forest zone in eastern Canada are proposed to offset the

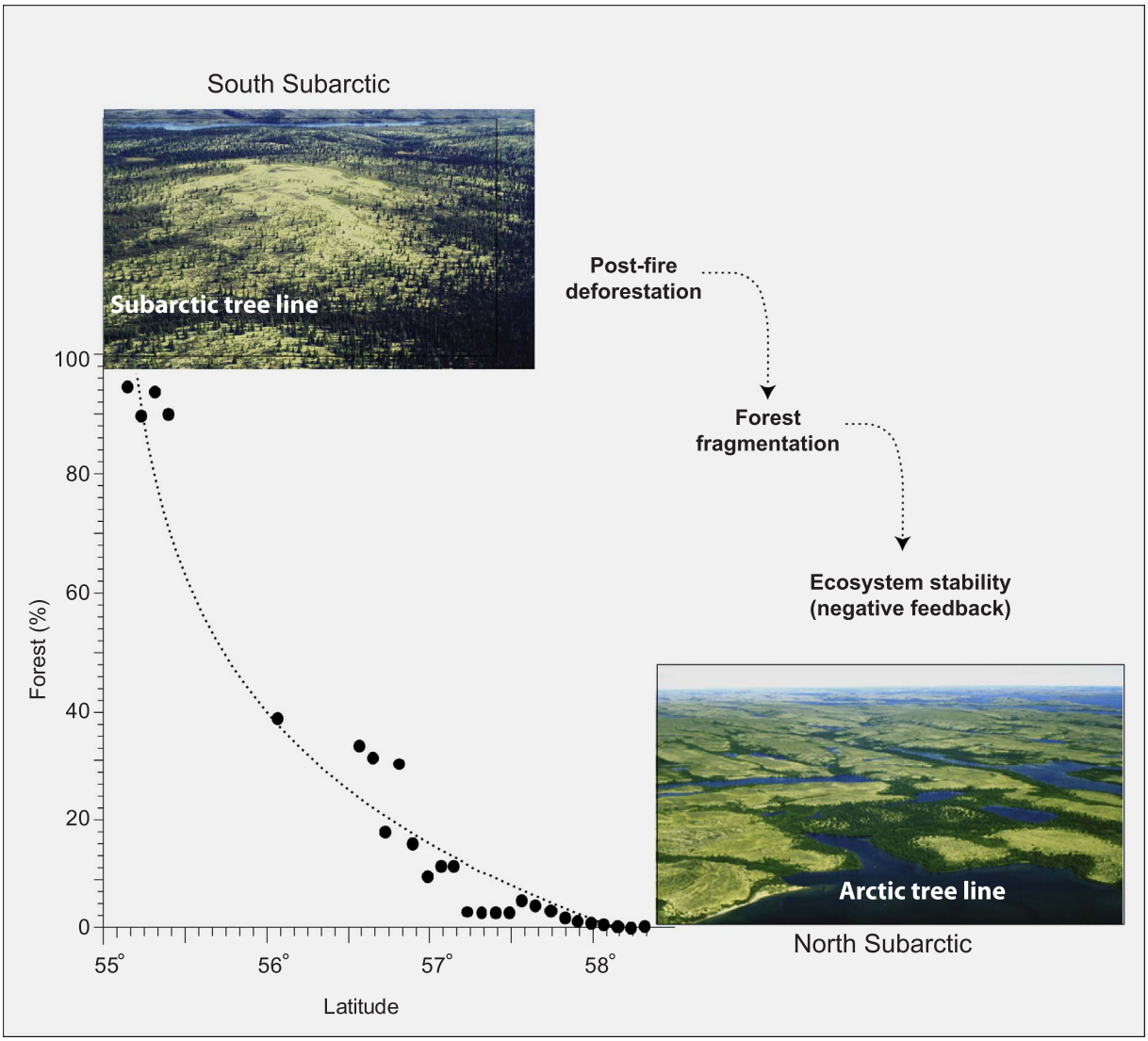

Fig. 11. Negative feedback loop resulting in a sharp decrease of fire frequency and size due to reduced combustible fuel caused by systematic deforestation of northernmost LWs (see Payette et al., 2001) over the last millennium and their transformation into lichen tundra communities above local Subarctic tree lines (upper panel). Preservation of isolated, relict, old-growth LWs (> 1000 year old) at the Arctic tree line (lower panel).

increased emission of atmospheric gases and thus mitigate climate change (Mansuy et al., 2013; Hébert et al., 2014). Silvicultural treatments are encouraged to increase the ecosystem resilience of LW by tree plantation (Tremblay et al., 2013; Hébert et al., 2014), which is considered as a management strategy to increase carbon sinks (Gonzalez et al., 2013). Because of the low density of trees in LWs, however, caution should be exercised in order to avoid frequent fire disturbances that may affect the feasibility of these projects (Mansuy et al., 2013).

7.1. Methods

Monitoring of daytime temperature (daily, every two hours) of closed forest (CF), lichen woodland (LW) and lichen hollow (LH) during June, July and August 1997 to 2015 made it possible to evaluate the impact of the forest structure on the thermal environment, and the climatic signature of the dominant vegetation covers of the boreal forest (47°40′N, 70°50′W). Temperature data loggers (StowAway® XTI and Hobo UA-001-08) were used to record temperature at 1 m above the ground in a closed-canopy spruce-moss forest (90% tree cover), a lichen-spruce woodland (25% tree cover) and a lichen hollow (0–1% tree cover) surrounded by lichen woodlands. The loggers were installed in the center of each site, and protected from exposure to direct sunlight and rain by white plastic devices facilitating free-air movement. Climatic data of the Quebec City area (Jean-Lesage Airport weather station, about 100 km west of the study area) were used to support the study site data for precipitation and temperature trends. The two forests are located 12 km apart, and the LH about 4 km away from them. The forests are 125 and 115 year old postfire stands growing on coarse-grained fluvio-glacial and till deposits on a gentle slope (3–9% gradient), about 700 m above sea level. The closed canopy forest consists of many closely spaced trees (generally < 3 m apart) with the shaded ground covered by mosses and shrubs.

Acknowledgements

We are most grateful to the authorities of the «Parc national des Grands-Jardins (SEPAQ)» for giving the permission to record climatic data over the last 20 years. Pierre-Luc Couillard and Jason Laflamme provided data on density of forest trees from the Quebec Government Forest Surveys. We acknowledge the Natural Sciences and Engineering Research Council of Canada (NSERC) through the Northern Research Chair Program for continuous financial support. Useful comments on an earlier version of this manuscript from anonymous reviewers were greatly appreciated.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.02.043.

References

Ahti, T., 1959. Studies on the caribou lichen stands of Newfoundland. Annales Botanici Societalis Zoologicae Botanicae Fennicae 'Vanamo' 30, 1–44.

Ahti, T., 1961. Taxonomic studies on reindeer lichens (Cladonia, sub-genus Cladina). Annales Botanici Societas 'Vanamo' 32, 1–160.

Arsenault, P., 1979. Effets allélopathiques causés par des lichens fruticuleux terricoles sur Picea mariana. M.Sc. Thesis. Université Laval. Québec, Canada.

Arseneault, D., Payette, S., 1992. A postfire shift from lichen-spruce to lichen-tundra vegetation at tree line. Ecology 73, 1067–1081.

Arseneault, D., Payette, S., 1997. Landscape change following deforestation at the arctic tree line in Québec, Canada. Ecology 78, 693–706.

Arseneault, D., Sirois, L., 1990. Forme et croissance de l'épinette noire (*Picea mariana* (Mill.) B.S.P.) avant et après-feu en toundra forestière. Naturaliste canadien 117, 1–7.

Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y., Deshaye, J., 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Québec: an application of fire history and Landsat data. J. Appl. Ecol. 34, 65–78.

Asselin, H., Payette, S., 2005a. Late Holocene opening of the forest tundra landscape in northern Québec, Canada. Glob. Ecol. Biogeogr. 14, 307–313.

Asselin, H., Payette, S., 2005b. Late Holocene deforestation of a tree line site: estimation of pre-fire vegetation composition and black spruce cover using soil charcoal. Ecography 28, 801–805.

Auclair, A.N.D., 1983. The role of fire in lichen-dominated tundra and forest-tundra. Pages 235–256 in The Role of Fire in Northern Circumpolar Ecosystems. Wein, R.W., MacLean, D.A., editors. SCOPE 18. John Wiley & Sons, New York, New York.

Auclair, A.N.D., 1985. Postfire regeneration of plant and soil organic pools in a *Picea mariana-Cladonia stellaris* ecosystem. Can. J. For. Res. 15, 279–291.

Auger, S., Payette, S., 2010. Four millennia of woodland structure and dynamics at the Arctic treeline of eastern Canada. Ecology 91, 1367–1379.

Bala, G., Caldeira, K., Wickett, M., Phillips, T.J., Lobell, D.B., Delire, C., Mirin, A., 2007. Combined climate and carbon-cycle effects of large-scale deforestation. Proc. Natl Acad. Sci. USA 104, 6550–6555.

Barry, R.G., 1967. Seasonal location of the Arctic front over North America. Geograp. Bull. 9, 79–95.

Barton, A.M., Grenier, D.J., 2008. Dynamics of jack pine at the southern range boundary in downeast Maine. Can. J. For. Res. 38, 733–743.

Bégin, C., Filion, L., 1999. Black spruce (*Picea mariana*) architecture. Can. J. Bot. 77, 664–672.

Bergerud, A.T., 1971. Abundance of forage on the winter range of Newfoundland caribou. Can. Field-Nat. 85, 39–52.

Bergerud, A.T., 1988. Caribou, wolves and man. Trends Ecol. Evol. 3, 68–72.

Bernier, P.Y., Desjardins, R.L., Karimi-Zindashty, Y., Worth, D., Beaudoin, A., Luo, Y., Wang, S., 2011. Boreal lichen woodlands: a possible negative feedback to climate change in eastern North America. Agric. For. Meteorol. 151, 521–528.

Betts, R.A., 2000. Offset of the potential carbon sink from boreal afforestation by decreases in surface albedo. Nature 408, 187–190.

Betts, A.K., Ball, J.H., 1997. Albedo over the boreal forest. J. Geophys. Res. 102, 28901–28909.

Bigras, F., Coursolle, C., Margolis, H.A., 2004. Survival and growth of *Picea glauca* seedlings as a function of freezing temperatures and exposure times during budbreak and shoot elongation. Scand. J. For. Res. 19, 206–216.

Birks, H.H., 2003. The importance of plant macrofossils in the reconstruction of lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. Quat. Sci. Rev. 22, 453–473.

Black, R.A., Bliss, L.C., 1978. Recovery sequence of *Picea mariana – Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. Can. J. Bot. 56, 2020–2030.

Black, R.A., Bliss, L.C., 1980. Reproductive ecology of *Picea mariana* (Mill.) B.S.P., at tree line near Inuvik, Northwest Territories Canada. Ecol. Monogr. 50, 331–354.

Bodine, D., Klein, P.M., Arms, S.C., Shapiro, A., 2009. Variability of surface air temperature over gently sloped terrain. J. Appl. Meteorol. Climatol. 48, 1117–1141.

Boiffin, J., Munson, A.D., 2013. Three large fire years threaten resilience of closed crown black spruce forests in eastern Canada. Ecosphere 4, art. 56.

Bonan, G.B., Pollard, D., Thompson, S.L., 1992. Effects of boreal forest vegetation on global climate. Nature 359, 716–718.

Boudreau, S., Payette, S., 2004a. Growth performance of *Cladina stellaris* following caribou disturbance in subarctic Quebec. Ecoscience 11, 347–355.

Boudreau, S., Payette, S., 2004b. Caribou-induced changes in species dominance of lichen woodlands: an analysis of plant remains. Am. J. Bot. 91, 422–429.

Brandt, J.P., 2009. The extent of the North American boreal zone. Environ. Rev. 17, 101–161.

Brodo, I.M., Duran Sharnoff, S., Sharnoff, S., 2001. Lichens of North America. Yale University Press, New Haven, Connecticut, U.S.A.

Brown, R.T.P., Mikola, P., 1974. The influence of fruticose soil lichens upon mycorrhizae and seedling growth of forest trees. Acta Forestalia Fennica 141, 1–22.

Bryson, R.A., 1966. Air masses, streamlines and the boreal forest. Geogr. Bull. 8, 228–269.

Bryson, R.A., Hare, F.K., editors, 1974. Climates of North America. World Survey of Climatology, Vol. 11. Elsevier Scientific Publishing Company. New York, U.S.A.

Carroll, S.B., Bliss, L.C., 1982. Jack pine-lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. Can. J. Bot. 60, 2270–2282.

Carstairs, A.G., Oechel, W.C., 1978. Effects of several microclimatic factors and nutrients on net carbon dioxide exchange in *Cladonia alpestris* (L.) Rabh. in the subarctic. Arct. Alp. Res. 10, 81–94.

Christiansen, J.S., 1988. A spruce-lichen woodland in northern Alaska: postfire regeneration and community dynamics. M.Sc. Thesis, University of Washington. Seattle, Washington, U.S.A.

Cogbill, C.V., 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. Can. J. For. Res. 15, 252–261.

Conkey, L.E., Keifer, M.B., Lloyd, A.H., 1995. Disjunct jack pine (Pinus banksiana Lamb.) structure and dynamics, Acadia National Park, Maine. Ecoscience 2, 168–176.

Coop, J.D., Givnish, T.J., 2007. Gradient analysis of reversed treelines and grasslands of the Valles Caldera, New Mexico. J. Veg. Sci. 18, 43–54.

Côté, M., Ferron, J., Gagnon, R., 2003. Impact of seed and seedling predation by small rodents on early regeneration establishment of black spruce. Can. J. For. Res. 33, 2362–2371.

Côté, M., Ferron, J., Gagnon, R., 2005. Invertebrate predation of postdispersal seeds and juvenile seedlings of black spruce (*Picea mariana*) in the boreal forest of eastern Canada. Can. J. For. Res. 35, 674–681.

Côté, D., Girard, F., Hébert, F., Bouchard, S., Gagnon, R., Lord, D., 2013. Is the closed-crown boreal forest resilient after successive stand disturbances? A quantitative demonstration from a case study. J. Veg. Sci. 24, 664–674.

Côté, D., Lupi, C., Gagnon, R., Lord, D., Morin, H., 2014. Growth dynamics of successive postfire cohorts of black spruce: is site potential reduced? Forest. Chron. 90, 96–104.

Couillard, P.-L., Payette, S., Grondin, P., 2012. Recent impact of fire on high-altitude balsam fir forests in south-central Quebec. Can. J. For. Res. 42, 1289–1305.

Coxson, D.S., Marsh, J., 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Can. J. Bot. 79, 1449–1464.

Cowles, S., 1982. Preliminary results investigating the effect of lichen ground cover on the growth of black spruce. Nat. Can. 109, 573–581.

Crawford, R.M.M., 1989. Studies in Plant Survival. Blackwell Scientific Publications, Oxford, U.K, Ecological Case Histories of Plant Adaptation to Adversity.

Crête, M., Morneau, C., Naud, R., 1990. Biomasse et espèces de lichens terrestres disponibles pour le caribou dans le nord du Québec. Can. J. Bot. 68, 2047–2053.

Crittenden, P.D., 1983. The role of lichens in the nitrogen economy of subarctic woodlands: nitrogen loss from the nitrogen-fixing lichen Stereocaulon paschale during rainfall. In: Lee, J.A., McNeill, S., Rorison, I.H., editors. Nitrogen as an Ecological Factor. Blackwell Scientific Publishers, Oxford, U.K., 43–68.

Crittenden, P.D., 1999. Aspects of the ecology of mat-forming lichens. Rangifer 20, 127–139.

Crittenden, P.D., Kershaw, K.A., 1978. Discovering the role of lichens in the nitrogen cycle in boreal-arctic ecosystems. The Bryologist 81, 258–267.

Delwaide, A., Filion, L., 1988. Les coupes forestières dans les pessières à lichens: effets sur la croissance et la régénération des conifères (Whapmagoostui, Québec subarctique). Can. J. Bot. 66, 1013–1020.

Desponts, M., Payette, S., 1992. Recent dynamics of jack pine at its northern distribution limit in northern Quebec. Can. J. Bot. 70, 1157–1167.

DesRochers, A., Gagnon, R., 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. 27, 1263–1267.

D'Orangeville, L., Duchesne, L., Houle, D., Kneeshaw, D., Côté, B., Pederson, N., 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science 352, 1452–1455.

Duchesne, S., Sirois, L., 1995. Phase initiale de régénération après feu des populations conifériennes subarctiques. Can. J. For. Res. 25, 307–318.

Dufour, B., Boucher, J.-F., Tremblay, P., Mailly, D., Lord, D., 2016. Black-spruce lichen woodlands growth and carbon drawdown potentials as revealed by mature stands. Boreal Environ. Res. 21, 71–86.

Dufour-Tremblay, G., Boudreau, S., 2011. Black spruce regeneration at the treeline ecotone: sygergistic impacts of climate change and caribou activity. Can. J. For. Res. 41, 460–468.

Dy, G., Payette, S., 2007. Frost hollows of the boreal forest as extreme environments for black spruce tree growth. Can. J. For. Res. 37, 492–504.

Dyrness, C.T., Norum, R.A., 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Can. J. For. Res. 13, 879–893.

Dyrness, C.T., Van Cleve, K., Levison, J.D., 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. Can. J. For. Res. 19, 1389–1396.

Engstrom, D.R., Hansen, B.C.S., 1985. Postglacial vegetational change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy. Can. J. Bot. 63, 543–561.

Fan, S.M., Goulden, M.L., Munger, J.W., Daube, B.C., Bakwin, P.S., Wofsy, S.C., Amthor, J.S., Fitzjarrald, D.R., Moore, K.E., Moore, T.R., 1995. Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. Oecologia 102, 443–452.

Filion, L., Payette, S., 1989. Subarctic lichen polygons and soil development along a colonization gradient on eolian sands. Arct. Alp. Res. 21, 175–184.

Fitzjarrald, D.R., Moore, K.E., 1994. Growing season boundary layer climate and surface exchanges in a subarctic lichen woodland. J. Geophys. Res. 99, 1899–1917.

Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest fires. Sci. Total Environ. 262, 221–229.

Flinn, M.A., Wein, R.W., 1977. Depth of underground plant organs and theoretical survival during fire. Can. J. Bot. 55, 1550–1554.

Flinn, M.A., Wein, R.W., 1988. Regrowth of forest understory species following seasonal burning. Can. J. Bot. 66, 150–155.

Foley, J.A., Kutzbach, J.E., Coe, M.T., Levis, S., 1994. Feedbacks between climate and

boreal forests during the Holocene epoch. Nature 371, 52–54.
Foster, D.R., 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. J. Ecol. 73, 517–534.
Foster, D.R., King, G.A., 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. J. Ecol. 74, 465–483.
Gajewski, K., Garralla, S., Milot-Roy, V., 1996. Postglacial vegetation at the northern limit of lichen woodland in northwestern Québec. Géographie physique et Quaternaire 50, 341–350.
Gajewski, K., Payette, S., Ritchie, J.C., 1993. Holocene vegetation history at the boreal-forest-shrub-tundra transition in north-western Quebec. J. Ecol. 81, 433–443.
Geiger, R., Aron, R.H., Todhunter, P., 2003. Climate Near the Ground. Rowman & Littlefield, Lanham.
Girard, F., Payette, S., Delwaide, A., 2017. Patterns of early postfire succession of alpine, subalpine and lichen-woodland vegetation: 21 years of monitoring from permanent plots. Forests 8, 346.
Girard, F., Payette, S., Gagnon, R., 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J. Biogeogr. 35, 529–537.
Girard, F., Payette, S., Gagnon, R., 2009. Origin of the lichen-spruce woodland in the closed-crown forest zone of eastern Canada. Glob. Ecol. Biogeogr. 18, 291–303.
Girard, F., Payette, S., Gagnon, R., 2011. Dendrochronological analysis of black spruce in lichen-spruce woodlands of the closed-crown forest zone in eastern Canada. Ecoscience 18, 279–294.
Gonzalez, E., Hébert, F., Boucher, J.-F., Sirois, P., Lord, D., 2013. Lichen-spruce woodland early indicators of ecological resilience following sylvicultural disturbances in Québec's closed-crown forest zone. Am. J. Plant Sci. 4, 749–765.
Grove, J.M., 2004. Little Ice Ages. Second edition. Routledge, Taylor & Francis Group, London, U.K, Ancient and Modern.
Hare, F.K., 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. Geogr. Rev. 40, 615–635.
Hare, F.K., 1959. A photo-reconnaissance survey of Labrador-Ungava. Department of Mines and Technical Surveys. Geographical Branch, Ottawa. Memoir 6, 1–83.
Hare, F.K., Ritchie, J.C., 1972. The boreal bioclimates. Geogr. Rev. 62, 333–365.
Hawkins, B.J., Guest, H.J., Kolotelo, D., 2003. Freezing tolerance of conifer seeds and germinants. Tree Physiol. 23, 1237–1246.
Hébert, F., Boucher, J.-F., Walsh, D., Tremblay, P., Côté, D., Lord, D., 2014. Black spruce growth and survival in boreal open woodlands 10 years following mechanical site preparation and planting. Forestry 87, 277–286.
Houle, G., Filion, L., 2003. The effects of lichens on white spruce seedling establishment and juvenile growth in a spruce-lichen woodland of subarctic Québec. Ecoscience 10, 80–84.
Hustich, I., 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. Acta Geographica 12, 1–48.
Hustich, I., 1957. On the phytogeography of the subarctic Hudson Bay lowland. Acta Geographica 16, 1–48.
Hustich, I., 1966. On the forest-tundra and the northern tree-lines. Annales Universitatis Turkuensis Series A II 36, 7–47.
Inouye, D.W., 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecol. Lett. 3, 457–463.
Jasinski, J.P.P., Payette, S., 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol. Monogr. 75, 561–583.
Jayen, K., Leduc, A., Bergeron, Y., 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. Ecoscience 13, 143–151.
Johnson, E.A., 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53, 2933–2941.
Johnson, E.A., 1981. Vegetation and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology 62, 200–215.
Johnson, E.A., Miyanishi, K., 1999. Subarctic lichen woodlands. In: Anderson, R.C., Fralish, J.S., Baskin, J.M., editors, Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York, U.S.A, p. 421–36.
Johnson, D., 2007. Dynamique de régénération de Picea mariana dans le domaine de la pessière ouverte à lichen au Québec nordique. M.Sc. Thesis, UQAR. Rimouski, Canada.
Johnstone, J.F., Chapin, F.S., 2006. Effects of soil burn severity on postfire tree recruitment in boreal forest. Ecosystems 9, 14–31.
Johnstone, J.F., Kasischke, E.S., 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. Can. J. For. Res. 35, 2151–2163.
Karlsson, I.M., 2000. Nocturnal air temperature variations between forest and open areas. J. Appl. Meteorol. 39, 851–862.
Kemball, K.J., Wang, G.G., Westwood, A.R., 2006. Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Can. J. For. Res. 36, 1943–1950.
Kershaw, K.A., 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. Can. J. Bot. 55, 393–410.
Kershaw, K.A., 1978. The role of lichens in boreal tundra transition areas. Bryologist 81, 294–306.
Kershaw, K.A., 1985. Physiological Ecology of Lichens. Cambridge University Press, Cambridge, U.K.
Kershaw, K.A., Field, G.F., 1975. Studies on lichen-dominated systems. XV. The temperature and humidity profiles in a *Cladina alpestris* mat. Can. J. Bot. 53, 2614–2620.
Kershaw, K.A., Rouse, W.R., 1971. Studies on lichen-dominated systems. II. The growth pattern of *Cladonia alpestris* and *C. rangiferina*. Can. J. Bot. 49, 1401–1410.
Kershaw, K.A., Rouse, W.R., 1976. The impact of fire on forest and tundra ecosystems. Final Report 1975. Arctic Land Use Research. Program Report 75-76-63.
Kershaw, K.A., Smith, M.M., 1978. Studies on lichen-dominated systems. XXI. The control of seasonal rates of net photosynthesis by moisture, light, and temperature in *Stereocaulon paschale*. Can. J. Bot. 56, 2825–2830.
King, G.A., 1993. Vegetation and pollen relationships in eastern Canada. Can. J. Bot. 71, 193–210.
Lafleur, P., Adams, P., 1986. The radiation budget of a subarctic woodland canopy. Arctic 39, 172–176.
Laliberté, A.-C., Payette, S., 2008. Primary succession of subarctic vegetation and soil on the fast-rising coast of eastern Hudson Bay, Canada. J. Biogeogr. 35, 1989–1999.
Lamb, H.F., 1985. Palynological evidence for postglacial change in the position of tree limit in Labrador, eastern Canada. Ecol. Monogr. 55, 241–258.
Langvall, O., Ottosson-Lofvenius, M., 2002. Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. Forest Ecol. Manage. 168, 149–161.
Larsen, J.A., 1980. The Boreal Ecosystem. Academic Press, New York, USA.
Lavoie, C., Payette, S., 1994. Recent fluctuations of the lichen spruce forest limit in subarctic Québec. J. Ecol. 82, 725–734.
Lavoie, L., Sirois, L., 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. J. Veg. Sci. 9, 483–492.
Lucarotti, C., 1976. Post-fire change in mycofloral species and mesofauna populations in lichen-woodland soils, Schefferville, Québec. M.Sc. Thesis. McGill University. Montréal, Québec, Canada.
MacLean, D.A., Woodley, S.J., Weber, M.G., Wein, R.W., 1983. Fire and nutrient cycling. In: Wein, R.W., MacLean, D.A., editors. The role of fire in Northern circumpolar ecosystems. SCOPE 18. John Wiley & Sons, New York, New York, 111–132.
Maikawa, E., Kershaw, K.A., 1976. Studies on lichen dominated systems. XIX. The postfire recovery sequence of black spruce-lichen woodland in the Abitau Lake region. Can. J. Bot. 54, 2674–2687.
Mansuy, N., Gauthier, S., Bergeron, Y., 2013. Afforestation opportunities when stand productivity is driven by a high risk of natural disturbance: a review of the open lichen woodland in the eastern boreal forest of Canada. Mitig. Adapt. Strat. Glob. Change 18, 245–264.
Messier, F., Huot, J., Le Henaff, D., Luttich, S., 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic 41, 279–287.
Moore, T.R., 1980. The nutrient status of subarctic woodland soils. Arct. Alp. Res. 12, 147–160.
Moore, T.R., 1981. Controls on the decomposition of organic matter in subarctic woodland soils. Soil Sci. 131, 107–113.
Moore, T.R., 1984. Litter decomposition in a subarctic spruce-lichen woodland, eastern Canada. Ecology 65, 299–308.
Morin, A., Payette, S., 1984. Expansion récente du mélèze à la limite des arbres (Québec nordique). Can. J. Bot. 62, 1404–1408.
Morneau, C., 1999. Analyse dendroécologique de l'activité du caribou et perturbation de la végétation dans le nord-est du Québec-Labrador. Ph.D. dissertation. Université Laval. Quebec City, Quebec, Canada.
Morneau, C., Payette, S., 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. Can. J. Bot. 67, 2770–2782.
Morneau, C., Payette, S., 1998. A dendroecological method to evaluate past caribou (*Rangifer tarandus* L.) activity. Ecoscience 5, 64–76.
Morneau, C., Payette, S., 2000. Long-term fluctuations of a caribou population revealed by tree-ring data. Can. J. Zool. 78, 1784–1790.
Moss, M., Hermanutz, L., 2009. Postfire seedling recruitment at the southern limit of lichen woodland. Can. J. For. Res. 39, 2299–2306.
Nieboer, E., Richardson, D.H.S., Tomassini, F.D., 1978. Mineral uptake and release by lichens: an overview. The Bryologist 81, 226–246.
Oke, T.R., 1987. Boundary Layer Climates. Cambridge University Press, Cambridge, U.K.
Ouimet, R., Boucher, J.-F., Tremblay, P., Lord, D., 2018. Comparing soil profiles of adjacent forest stands with contrasting tree densities: lichen woodlands vs. black spruce–feathermoss stands in the continuous boreal forest. Can. J. Soil Sci. (Submitted for publication).
Payette, S., 1983. The forest-tundra and present tree-lines of the northern Québec-Labrador peninsula. In: Tree-line Ecology, Proceedings of the Northern Québec Tree-Line Conference. Morisset, P., Payette, S., editors. Nordicana 47, pp. 3–23.
Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B., editors, A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, U.K., pp. 144–165.
Payette, S., Bhiry, N., Delwaide, A., Simard, M., 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Can. J. For. Res. 30, 288–305.
Payette, S., Delwaide, A., 2003. Shift of conifer boreal forest to lichen-heath parkland caused by successive stand disturbances. Ecosystems 6, 540–550.
Payette, S., Delwaide, A., Couillard, P.-L., Pilon, V., 2017. Disjunct jack pine (*Pinus banksiana*) populations of the boreal forest in eastern Canada: expanding, declining or stable? Botany 95, 697–707.
Payette, S., Delwaide, A., Simard, M., 2010. Frost-ring chronologies as dendroclimatic proxies of boreal environments. Geophys. Res. Lett. 37, L02711.
Payette, S., Filion, L., Delwaide, A., 2008. Spatially explicit fire-climate history of the boreal forest-tundra (eastern Canada) over the last 2000 years. Philos. Trans. Roy. Soc. B 363, 2301–2316.
Payette, S., Fortin, M.-J., Gamache, I., 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. Bioscience 51, 709–718.
Payette, S., Gagnon, R., 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. Nature 313, 570–572.
Payette, S., Morneau, C., 1993. Holocene relict woodlands at the eastern Canadian treeline. Quat. Res. 39, 84–89.

Payette, S., Boudreau, S., Morneau, C., Pitre, N., 2004. Long-term interactions between migratory caribou, wildfires and Nunavik hunters inferred from tree rings. Ambio 33, 482–486.
Pegau, R.E., 1970. Effect of reindeer trampling and grazing on lichens. J. Range Manag. 23, 95–97.
Plasse, C., Payette, S., 2015. Frost hollows of the boreal forest: a spatiotemporal perspective. J. Ecol. 103, 669–678.
Pollock, S.L., Payette, S., 2010. Stability in the patterns of long-term development and growth of the Canadian spruce-moss forest. J. Biogeogr. 37, 1684–1697.
Rencz, A.N., 1976. The Level and Distribution of Biomass and Nutrients in a Subarctic Lichen Woodland. Thesis, Biology Department, McGill University, Montréal, Canada, M.Sc.
Rencz, A.N., Auclair, A.N.D., 1978. Biomass distribution in a subarctic *Picea mariana – Cladonia alpestris* woodland. Can. J. For. Res. 8, 168–176.
Richard, P.J.H., 1995. Le couvert végétal du Québec-Labrador il y a 6000 ans BP: essai. Géographie physique et Quaternaire 49, 117–140.
Ritchie, J.C., 1959. The Vegetation of Northern Manitoba, III: Studies in the subarctic. Technical Paper Number 3, Arctic Institute of North America, Montreal, Canada.
Ritchie, J.C., 1987. Postglacial Vegetation of Canada. Cambridge University Press, Cambridge, UK.
Riverin, S., Gagnon, R., 1996. Dynamique de la régénération d'une pessière à lichen dans la zone de la pessière noire à mousses, nord du Saguenay-Lac-Saint-Jean (Québec). Can. J. For. Res. 26, 1504–1509.
Rouse, W.R., 1976. Microclimate changes accompanying burning in subarctic lichen woodland. Arct. Alp. Res. 8, 357–376.
Rouse, W.R., Kershaw, K.A., 1971. The effects of burning on the heat and water regimes of lichen-dominated subarctic surfaces. Arct. Alp. Res. 3, 291–304.
Rousseau, J., 1952. Les zones biologiques de la péninsule Québec-Labrador et l'hémiarctique. Can. J. Bot. 30, 436–474.
Rousseau, J., 1968. The vegetation of the Québec-Labrador peninsula between 55° and 60° N. Naturaliste Can. 95, 469–563.
Rowe, S.J., 1972. Forest Regions of Canada. Canada Forestry Service Publication 1300, Ottawa, Canada.
Rowe, S.J., 1984. Lichen woodland in northern Canada. In: Ecology, Northern, Management, Resource, Olson, R., Geddes, F., Hastings, R. (Eds.), University of Alberta Press. Edmonton, Alberta, pp. 225–237.
Rudolph, T.D., Laidly, P.R., 1990. Pinus banksiana Lamb. Jack pine. In: Burns, R.M., Honkala, B.H., editors. Silvics of North America. USDA Forest Service, Washington, D.C.,
Sakai, A., Larcher, W., 1987. Frost Survival of Plants. Springer-Verlag, Berlin.
Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H., Chapin, F.S.I.I.I., 2012. Thresholds for boreal biome transitions. Proc. Natl. Acad. Sci. United States 109, 21384–21389.
Scotter, G.W., 1964. Effect of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. Canadian Wildlife Service, Wildlife Management Bulletin, Series 1, No. 18.
Sedia, E.G., Ehrenfeld, J.G., 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey pinelands. Oikos 100, 447–458.
Sharma, S., Couturier, S., Côté, S.D., 2009. Impacts of climate change on the seasonal distribution of migratory caribou. Glob. Change Biol. 15, 2549–2562.
Sirois, L., 1992. The transition between boreal forest and tundra. In: Shugart, H.H., Leemans, R., Bonan, G.B. editors. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, U.K., pp. 196–215.
Sirois, L., 1993. Impact of fire on *Picea mariana* and *Pinus banksiana* seedlings in subarctic lichen woodlands. J. Veg. Sci. 4, 795–802.
Sirois, L., 1995. Initial phase of postfire forest regeneration in two lichen woodlands of northern Québec. Ecoscience 2, 177–183.
Sirois, L., Payette, S., 1989. Postfire black spruce establishment in subarctic and boreal Quebec. Can. J. For. Res. 19, 1571–1580.
Sirois, L., Payette, S., 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Québec. Ecology 72, 619–627.
Skatter, H.G., Kansas, J.L., Charlebois, M.L., Balicki, B., 2014. Recovery of terrestrial lichens following wildfire in the boreal shield of Saskatchewan: early seral forage availability for woodland caribou (*Rangifer tarandus caribou*). Can. Wildl. Biol. Manage. 3, 1–14.
Steijlen, I., Nilsson, M.-C., Zackrisson, O., 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. Can. J. For. Res. 25, 713–723.
Stenroos, S., Velmala, S., Pykälä, J., Ahti, T., 2016. Lichens of Finland. Norrlinia 30, 1–896.
St-Pierre, H., Gagnon, R., Bellefleur, P., 1992. Régénération après feu de l'épinette noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale. Can. J. For. Res. 22, 474–481.
Sulyma, R., Coxson, D.S., 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia. Bryologist 104, 505–516.
Sutinen, M.-L., Arora, R., Wisniewski, M., Ashworth, E., Strimbeck, R., Palta, J., 2001. Mechanisms of frost survival and freeze-damage in nature. In: Bigras, F.J., Colombo, S.J., editors. Conifer Cold Hardiness. Kluwer Academic Publishers. Dordrecht, pp. 89–120.
Sveinbjörnsson, B., 1987. Reindeer lichen productivity as a function of mat thickness. Arct. Alp. Res. 19, 437–441.
Tegler, B., Kershaw, K.A., 1980. Studies on lichen-dominated systems. XXIII. The control of seasonal rates of net photosynthesis by moisture, light and temperature in *Cladonia rangiferina*. Can. J. Bot. 58, 1851–1858.
Thomson, J.W., 1967. The Lichen Genus *Cladonia* in North America. University of Toronto Press, Toronto, Canada.
Timoney, K.P., 1988. A geobotanical investigation of the subarctic forest-tundra of the Northwest Territories. Ph.D. Thesis. University of Alberta, Edmonton, Alberta, Canada.
Timoney, K.P., La Roi, G.H., Dale, M.R.T., 1993. Subarctic forest-tundra vegetation gradients: the sigmoid wave hypothesis. J. Veg. Sci. 4, 387–394.
Timoney, K.P., Wein, R.W., 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic 44, 223–230.
Tishkov, A., 2002. Boreal forests. In: The Physical Geography of Northern Eurasia. M. Shahgedanova, ed. Oxford University Press, Oxford, England, pp. 216–234.
Tømmervik, H., Johansen, B., Tombre, I., Thannheiser, D., Høgda, K.A., Gaare, E., Wielgolaski, F.E., 2004. Vegetation changes in the Nordic Mountain Birch Forest: the influence of grazing and climate change. Arct. Antarct. Alp. Res. 36, 323–332.
Tremblay, P., Boucher, J.-F., Tremblay, M., Lord, D., 2013. Afforestation of boreal open woodlands: early performance and ecophysiology of planted black spruce seedlings. Forests 4, 433–454.
Veilleux-Nolin, M., Payette, S., 2012. Influence of recent fire season and severity on black spruce regeneration in spruce-moss forests of Quebec, Canada. Can. J. For. Res. 42, 1316–1327.
Vézeau, C., Payette, S., 2016. Gap expansion in old-growth subarctic forests: the climate-pathogen connection. New Phytol. 212, 1044–1056.
Viereck, L.A., 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: Wein, R.W., MacLean, D.A., editors. The Role of Fire in Northern Circumpolar Ecosystems. SCOPE 18. John Wiley & Sons, New York, New York, pp. 201–220.
Vincent, A.B., 1965. Black Spruce: a review of its silvics, ecology and sylviculture. Department of Forests. Publication 1100. Ottawa, Ontario, Canada.
Vors, L.S., Boyce, M.S., 2009. Global declines of caribou and reindeer. Glob. Change Biol. 15, 2626–2633.
Wein, R.W., 1975. Vegetation recovery in arctic tundra and forest-tundra after fire. Canadian department of Indian and Northern Affairs. ALUR Report 74-75. Ottawa, Canada.
Wilton, W.C., 1963. Black spruce seedfall immediately following a fire. The Forestry Chronicle 39, 477–478.
Yarranton, G.A., 1975. Population growth in *Cladonia stellaris* (Opiz Pouz. And Vezda). New Phytologist 75, 99–110.
Zalatan, R., Gunn, A., Henry, G.H.R., 2006. Long-term abundance patterns of barren-ground caribou using trampling scars on roots of *Picea mariana* in the Northwest Territories. Arct. Antarct. Alp. Res. 38, 624–630.
Zamfir, M., 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. Oikos 88, 603–611.
Zasada, J., 1971. Frost damage to white spruce cones in interior Alaska. Research Note PNW-149 U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, Oregon, USA.